

THE ARGYROLAGIDAE, EXTINCT SOUTH AMERICAN MARSUPIALS

GEORGE GAYLORD SIMPSON

ABSTRACT

1. The known *Argyrolagidae* include two genera, for which the names *Microtragulus* and *Argyrolagus* are provisionally retained, with certainly four, possibly five or six valid species. *M. reigi* and *A. scagliai* are here described as new. The known range is mid or late Pliocene to early or mid Pleistocene in Argentina.

2. The dentition is $\frac{2-0-1-4}{2-0-1-4}$; incisors enlarged, procumbent below; all teeth rootless. The skulls have tubular bony snouts in advance of the incisors, a large, covered masseteric origin in the anterior part of the orbit, no distinct temporal fossa, and globular crania with somewhat inflated ear regions. Forelegs are reduced, hindlegs elongate; tibia and fibula are fused distally; metatarsals III and IV are appressed; there are only two digits in the pes; locomotion was bipedal ricochet. The habitus is remarkably convergent toward some placentals, especially kangaroo rats and jerboas.

3. Argyrolagids are marsupials but show no clear affinity with any others known. They probably arose from didelphids independently of other known families and are distinct at the superfamily level, at least.

4. Although early steps in argyrolagid ancestry and specialization are unknown, they probably became differentiated in South America, and there is no evidence or present reason to postulate that they have ever occurred elsewhere. They do not

indicate direct or indirect connection with Australia or the presence of a Southern Hemisphere bridge or intervening land.

5. Argyrolagids represent a distinct ecological habitus also found among independently evolved placentals in North America, Africa, Asia, and Australia (there also placental, not marsupial). The living animals of this habitus are characteristic of, although not confined to, deserts. The argyrolagids probably evolved also in adaptation to more or less local desert habitats, although the few specimens so far found were apparently not living under true desert conditions but marginally, in areas perhaps semiarid but not fully arid.

6. Argyrolagids (along with necrolestids and groeberiids) demonstrate that marsupial radiation in South America was even wider than indicated by the four families, Didelphidae, Borhyaenidae, Caenolestidae, Polydolpidae, usually considered in this connection. Prior to Pliocene-Recent invasions, all South American carnivores were marsupials, all medium to large herbivores were placentals, and other ecological niches were divided between placentals and marsupials, some of the latter, such as the argyrolagids, having extreme adaptive specializations. Marsupial radiation was almost as broad and reached almost as great extremes in South America as in Australia, the most important over-all difference being that in the latter continent the medium to large herbivores were marsupials.

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INTRODUCTION

The Argyrolagidae, also sometimes called the Microtragulidae, have been known after a fashion since 1904. After a fashion, only, for something has been lacking in knowledge of animals that have been considered rodents, ruminant artiodactyls, lagomorphs, notoungulates, diprotodont marsupials, paucituberculate marsupials, and polyprotodont marsupials, each after sober consideration by a qualified vertebrate paleontologist. That confusion had several causes. First, until the 1950's the animals were known only from isolated scraps. (The discoveries of the 1950's and later are here described for the first time.) Second, dissociated fragments, mainly metatarsals and mandibles, violated the Cuvierian "law" of association; it was impossible for a rational student to predict one part from another. Third, each part was decidedly *sui generis*, unlike anything else known. And fourth, in spite of that uniqueness, each part had certain (convergent, as we now know) broader similarities to various unrelated groups of mammals.

It is now possible to bring much, al-

though not yet quite complete, order out of that confusion. First, skulls, mandibles, and considerable parts of skeletons are now known. Second, indubitable association can now be established among the diverse anatomical parts. Third, the oddity of the group is enhanced rather than lessened by these discoveries, but that makes its definition all the sharper. Fourth, it has thus become possible to identify most merely convergent resemblances as such.

There thus comes clearly into view, after all those years, a fascinating and absolutely unique group of marsupials that has evolved in a direction unlike any other marsupials or indeed any other mammals in South America, and yet in doing so has occupied ecological niches resembling those of unrelated, or only distantly related, groups elsewhere in the world. On this and other evidence, it is also becoming increasingly evident that marsupial radiation in South America was considerably more complex than has been generally realized. That, in turn, raises interesting evolutionary and biogeographical problems.

All of the measurements, in text and tables, are given in millimeters. In the tables L=length and W=width. The following abbreviations are used:

MMMP, Museo Municipal . . . de Mar del Plata (full name noted below).

MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (also known, e.g. in publication by L. Kraglievich, as the "Museo Nacional"), Buenos Aires.

ACKNOWLEDGMENTS

The discoveries that now add so enormously to our knowledge of this family were all made in the Chapadmalal-Miramar region, along the shore line exposures between Punta Mogotes and Punta Hermingo (southwest of Mar del Plata) under the auspices of the Museo Municipal de Ciencias Naturales y Tradicional de Mar

del Plata, Buenos Aires Province, Argentina. Most of the discoveries were made personally by Galileo Scaglia, Director of that Museum. Sr. Scaglia has made all the pertinent materials of that museum available for this study and has supplied excellent, detailed field data for each specimen. The very possibility of this work, along with its details of field occurrence, is thus due to him. Osvaldo Reig worked for a time in collaboration with Sr. Scaglia and also found some of the specimens here described. More recently he had planned to describe these materials himself, and, although he had not yet compiled any notes or manuscript, a number of illustrations in various stages toward completion were made under his direction. When he left Argentina to go first to the United States and then to Venezuela, he found it impossible to continue that research. He then most generously turned it over to me, arranging for delivery to me of the specimens, and also placing his illustrations at my disposal. I urged Dr. Reig to let his name appear as co-author of this monograph, but he firmly declined on the grounds that he would be unable to do any of the actual research. It must nevertheless be recorded that the study would not have been made by me or at this time if it had not been for Dr. Reig. Bryan Patterson had also long been interested in these materials, and it was hoped for a time that he might undertake their study either alone or with me, but he waived his prior rights and insistently transferred the research to me.

Sr. Carlos Rusconi kindly supplied information on the type of *Argyrolagus parodii* Rusconi and gave me two unpublished photographs of that specimen. For functional comparisons data were provided by Dr. William D. Turnbull, Field Museum of Natural History, and Dr. Richard G. Van Gelder, American Museum of Natural History. The latter also provided a dipodid skeleton. Other specimens for comparison have been made available in the division

of mammals of the Museum of Comparative Zoology, Harvard University, and from the zoological collections of the Department of Biology, University of Arizona. Drawings are by RaVae Marsh.

Most of this study was carried out under professorships, half-time each, in the Museum of Comparative Zoology, Harvard University, and the Department of Geology, University of Arizona. This monograph is a joint contribution from these institutions.

CLASSIFICATION

Superfamily Argyrolagoidea

The only known members of this taxon are the Argyrolagidae. It is sufficiently characterized by the diagnosis of that family and description of its members that follow. Justification for ranking as a superfamily is given in a later section on affinities.

Family Argyrolagidae Ameghino, 1904

Argyrolagidae Ameghino, 1904, vol. 58, p. 255.
Microtragulidae Reig, 1955, p. 61.

Type. *Argyrolagus* Ameghino, 1904.

Referred genus. *Microtragulus* Ameghino, 1904.

Known distribution. Late (possibly middle) Pliocene to early (possibly middle) Pleistocene, "Araucanian" to San Andrés Formation, Argentina.

Diagnosis. Small marsupials with dental formula $\frac{2.0.1.4}{2.0.1.4}$. Teeth hypselodont, root-

less. Upper incisors recumbent and lower procumbent, forming a pinching apparatus. Presumed premolars small, nearly styliform. Upper molars simple, rounded lingually and flattened labially. Lower molars bilobed, anterior lobe larger, separation of lobes definite labially but may be obscure or absent lingually. Rostrum projecting well anterior to palate and incisors. Enormous palatal vacuities. Cranium inflated, with epitympanic and bullar cavities. Mandible with small coronoid process,

relatively low condyle, and inflected angle. Anterior limbs small. Three main segments of posterior limbs greatly elongated. Only two functional metatarsals and toes. Locomotion probably ricochetal.

Generic and family nomenclature. Ameghino proposed the then new generic and specific names *Microtragulus argentinus* and *Argyrolagus palmeri* in the same paper (Ameghino, 1904). That paper was distributed as a unit with serial pagination, but its original publication was in six different installments extending over three volumes of a journal. The two genera and species were published in the same volume and year, but *Microtragulus argentinus* was in an earlier issue and therefore has definite temporal, and not only page, priority.

In the original publication, *Microtragulus* was referred to the artiodactyl family Tragulidae, with which it has nothing to do as is now evident, although the misinterpretation was almost inevitable at the time. The type and then only species was based on a supposed cannon bone, apparently fused metatarsals, which are indeed similar to those of some advanced artiodactyls. *Argyrolagus*, its type based on a mandible obviously not artiodactyl but somewhat rodentlike, was made the sole member of a then new proposed family Argyrolagidae. Until 1955 no other name for a family including either of these generic names was proposed. Rusconi (1936) suggested that *Argyrolagus* and *Microtragulus* are synonymous, but he did not note that in that case *Microtragulus* would have priority, and he continued to use the names *Argyrolagus* and Argyrolagidae. Reig (1955, 1958) indicated *Argyrolagus* as a junior synonym of *Microtragulus* and used the family name Microtragulidae. No explanation was given, but it was evident (and has been confirmed in personal communication) that *Microtragulus* was considered as a senior synonym of *Argyrolagus* and therefore the valid name for what was believed to be

the sole genus of the family. The family name was changed to accord with the only supposedly valid generic name. That common sense procedure was then usual and was not contradicted by any rule or usage, although it has since been modified, contrary to common sense or earlier usage, by the Code of Nomenclature later promulgated (Stoll *et al.*, 1961, revised 1964).

There has been no first-hand study of this group since Rusconi (1933, 1936). Romer (1966, p. 379) listed it as "Microtragulidae, *Microtragulus* [*Argyrolagus*]" (square brackets in the original). Rusconi (1967) continued to use the name Argyrolagidae, appearing somewhat less positive that *Argyrolagus* and *Microtragulus* are synonymous and continuing to ignore the fact that *Microtragulus* has priority. He again tentatively puts forward that synonymy and does recognize that priority in later personal communication.

The situation, never clear, is now further obscured by the fact that there are definitely two genera and at least four species, possibly as many as six, among the known specimens. One cannot therefore simply take it that *Microtragulus* is a senior synonym of *Argyrolagus* and decide the family name on that basis, a decision that would be equivocal enough under the peculiar provisions of the current code. That two genera exist is established on the basis of mandibles and lower dentitions, none of them from the same locality or horizon as the types of *M. argentinus* and *A. palmeri*. One of these genera known from other materials does, in all probability, include *A. palmeri*. The problem at the generic level is that it is unknown whether *M. argentinus* also belongs to that genus, in which case *Argyrolagus* is a synonym of *Microtragulus*, or whether it belongs to the other genus known from mandibles from other horizons and localities, in which case both *Microtragulus* and *Argyrolagus* are valid names.

A direct and positive solution to this problem will require finding metatarsals

clearly referable to *M. argentinus* and a mandible of the same individual. The mandible presumably would then indicate whether the type of *M. argentinus* is or is not congeneric with the mandible type of *A. palmeri* and whether it does or does not belong to the second genus known from dentitions. One may hope for such a solution but cannot reasonably expect it in the near future, at least—well over sixty years have elapsed without the production of a single scrap of an argyrolagid, let alone associated skull and limb bones, from the type deposit of *Microtragulus* and *Argyrolagus*.

In the meantime, only quite indirect comparisons are possible. Metatarsals are known from only one individual of this family aside from the type of *M. argentinus*. Fortunately in that one instance, MMMP No. 785-S, from the Chapadmalal formation, the bones are individually associated with a mandible. The mandible is considered congeneric but not conspecific with the type of *A. palmeri*. The metatarsals of that individual are morphologically like the type *M. argentinus* but are 25 per cent larger, a difference not impossible but improbable within a single species.

The second genus now known to belong to this family (whatever names may be given to the genera and the family) occurs at an "Araucanian" horizon probably earlier and almost certainly not later than Ameghino's types from Monte Hermoso, and also in the Chapadmalal to the San Andrés formations in the Chapadmalal-Miramar region, beds younger than Monte Hermoso. Hence that genus must also have existed in Monte Hermoso time. The known specimens of jaws and cheek teeth are all definitely smaller than those of *A. palmeri* and others considered congeneric with the latter, including MMMP No. 785-S. Hence there is at least a possibility that the small metatarsals, type of *M. argentinus*, belong to the second genus (i.e. not to be the same genus as *A. pal-*

meri), for which *Microtragulus* would then be the valid generic name.

In MMMP No. 785-S the ratio of the length of the metatarsals to the length of M_{1-4} is 4.19. If the ratio were the same in an individual represented by a lower dentition from the San Andrés Formation (MMMP No. 960-M) belonging to the second genus, its metatarsals would be 26.4 mm in length. The length of the type *M. argentinus* is 28.5, only 9 per cent longer. Such little cogency as this very incomplete, very indirect comparison has, is, however, still further reduced by the facts that the San Andrés and Monte Hermoso individuals are quite unlikely to be conspecific, if only because there is a considerable difference in age, that they might well have had different limb-tooth proportions, and that similarity in length of metatarsals is not in any case a convincing generic character.

There is no possible objective solution to this problem. Any definite choice as to recognition and naming of the taxa at present must be purely arbitrary. Most clear-cut would be the tempting solution of having all the previous generic and family names officially rejected and then starting anew. In fact, the specific names, as will soon appear, are hardly in better shape and might be included in the holocaust. However, so radical an action is not likely to be accepted by the International Commission, would require long and costly argument and action, and even if officially approved, would be personally condemned by many zoologists.

I therefore propose action no less arbitrary but more conservative. I shall assume, until and unless contrary evidence is discovered, that the type of *Microtragulus argentinus* belongs to my "other genus" including "*Argyrolagus*" *catamarcensis* Kraglievich and MMMP No. 960-M (named *Microtragulus reigi* on a later page). On that assumption, *Microtragulus* is not synonymous with *Argyrolagus*. This

arbitrary assumption has these advantages:

It validates both of Ameghino's classic names for current continued usage, avoiding the necessity of coining any new generic names.

It validates the prior (by 51 years) family name and avoids a choice between family names that would be equivocal or insoluble under the current Code.

Nothing is known in definite contradiction of this usage. A final objective settlement, if one is ever achieved, is as likely to support this usage as to upset it. The chances are that any change that may later become necessary will be as slight under this usage as under any other.

Specific nomenclature. The status of the various previously proposed and here new specific names will be more particularly discussed under the following generic and specific headings. Here it may be pointed out in a more general way that this also is a problem that cannot at present be satisfactorily solved and can only be treated in a somewhat arbitrary way.

Four specific names have previously been proposed: *Microtragulus argentinus* Ameghino, 1904; *Argyrolagus palmeri* Ameghino, 1904; *Argyrolagus catamarcensis* Kraglievich, 1931; and *Argyrolagus parodii* Rusconi, 1933. The type of the first is not comparable with any of the others among these types. It is directly comparable with only one other known specimen, from which it differs specifically, at least. Indirect comparisons at the specific level are practically worthless. The type of *A. palmeri* is not at hand, although it may still be in existence. Available figures and descriptions of it seem to be adequate for comparison. The type of the last named species, *A. parodii*, has been virtually destroyed and available data are inadequate. Only for "*Argyrolagus*" *catamarcensis*, which proves to be a valid

species but not to belong to *Argyrolagus*, is an adequate type actually in hand. In the collections here first described there are two clear-cut genera and species. The species are distinct from "*A.*" *catamarcensis* but one is considered congeneric with the latter. Comparisons of the species with *M. argentinus*, *A. palmeri*, and *A. parodii* are unsatisfactory and inconclusive because of the noted deficiencies of these types. I have more or less arbitrarily given new names to the fully definable and distinctive species in the new collection. As previously noted, I have with even greater arbitrariness here assigned Ameghino's two generic names to the two genera recognized in the hitherto undescribed materials.

The facts that the teeth are continuously growing and that the sequence of size is also a morphological sequence (see Figure 1) suggest the possibility that the apparent generic and specific distinctions are in fact merely functions of individual age in a smaller number of taxa, perhaps even in one species. The possibility cannot be absolutely ruled out, but it is quite improbable. The larger species have more, and more distinct, vertical grooves (or flexids) on the lower molars, whereas it is a rule with few, perhaps no, exceptions in mammals that these tend either to disappear or to become fossetids with increasing age (wear). There are certain other structural differences, such as the proportions of trigonid and talonid lengths, that are not likely to change individually in just this way. Size differences in lower jaws are not associated with other evidence of individual age differences. In all known specimens M_4^1 have erupted and are worn. Teeth measurable at the wear surface and the alveolar end are not distinctly larger at the latter end. Limb bones with fused epiphyses are of markedly different sizes, indicating that size differences are not in all, if in any, instances caused by growth. The apparently different species are in part from different geological horizons.

Distribution: The known distribution of named taxa is as follows:

Chapadmalal-Miramar area, Buenos Aires Province	Monte Hermoso, Buenos Aires Province	Catamarca Province
San Andrés Formation: <i>Microtragulus reigi</i>		
Barranca de los Lobos Formation: <i>Microtragulus reigi</i>		
Vorohué Formation: <i>Microtragulus reigi</i>		
Chapadmalal Formation: <i>Microtragulus reigi</i> <i>Argyrolagus scagliai</i>	Monte Hermoso Formation: <i>Microtragulus argentinus</i> <i>Argyrolagus palmeri</i>	?Andalhualá member or formation (in the "Araucanian"): <i>Microtragulus catamarcensis</i>

The exact level of ?*Argyrolagus parodii* is unknown. It is probably from either the Chapadmalal or the Vorohué Formation and is surely from within the indicated Chapadmalal-Miramar sequence.

The Chapadmalal Formation, as restricted by Kraglievich (1952), is probably basal Pleistocene in age, now that Blancan in North America and Villafranchian in Europe are generally considered Pleisto-

cene rather than Pliocene as sometimes earlier designated. The three overlying formations in which argyrolagids occur do not seem to cover any considerable span of time and are probably also early Pleistocene but could just possibly extend into the middle Pleistocene. Actual superposition of Chapadmalal on Monte Hermoso has not been demonstrated, but Monte Hermoso is generally considered somewhat older, and hence Upper Pliocene, on faunal grounds. "Araucanian" is an obsolescent and inappropriate name for a long sequence of mainly Pliocene beds. It seems to include strata of Monte Hermoso age, but also some distinctly older. The type of *M. catamarcensis* is labeled "Andalhualá," presumably for the locality, and may well be from the beds so named with that as type locality. If so, the age of this type is probably pre-Monte Hermoso and approximately middle Pliocene.

Genus *Microtragulus* Ameghino

Microtragulus Ameghino, 1904, vol. 58, p. 191.

Type. *Microtragulus argentinus* Ameghino.

Referred species. *M. catamarcensis* Kraglievich and *M. reigi*, new species.

Known range. Upper (or possibly Middle) Pliocene to Lower (or possibly Middle) Pleistocene, Argentina.

Diagnosis. (For reasons explained elsewhere, this diagnosis is arbitrarily based on the referred and not the type species.) M_{1-3} with rounded lingual faces, internal groove absent or slight, external groove present, relatively posterior, partially distinct second lobe short and wide. These teeth almost as wide as long. M_4 elongate, distinctly bilobed, second lobe narrow.

Discussion. The above characters, shared by *M. catamarcensis* and *M. reigi*, sharply distinguish those species from *Argyrolagus palmeri* and *A. scagliai*. The teeth are more fully described and other morphological distinctions are mentioned in the anatomical section of this study.

Microtragulus argentinus Ameghino

Microtragulus argentinus Ameghino, 1904, vol. 58, p. 191; 1906, fig. 344.

Type MACN No. 4743, metatarsals III-IV and associated tarsal bones.

Hypodigm. Type only.

Known range. Monte Hermoso Formation, Monte Hermoso, Buenos Aires Province.

Original diagnosis (of genus and species). "The smallest of known artiodactyls, since its size did not exceed that of a small rat. . . . The metatarsal or cannon bone, formed by the fusion of the two median metatarsals III and IV, is only 27 mm long and 2 mm wide in its narrowest middle part. . . . The two metatarsals in question . . . are fused for their whole length but between the two there remains a deep longitudinal groove in the anterior face and another, shallower, on the posterior face. The lateral metatarsals II and V are atrophied, represented only by their styliform proximal ends, this part of metatarsal V being fused with that of metatarsal IV, but that of metatarsal II remained separate. The cuboid, scaphoid [navicular], and cuneiforms are separate, but are constructed, like the other bones, on the same type as that of the Tragulidae."¹ (Parts of the diagnosis merely descriptive of

Hypisodus and now known to be irrelevant are omitted.)

Discussion. The name is not known to be preoccupied, was the first ever applied to a member of this family, and was given a definition technically sufficient under the Code. It is therefore necessarily valid as a name. However, the diagnosis, which is relative to tragulids and to *Hypisodus* (a hypertragulid), placental artiodactyls, is simply irrelevant now that *Microtragulus* is known to be a marsupial. Direct comparison is possible only with the type of *Argyrolagus scagliai*. The metatarsals (not in fact fused) agree except that those of the latter are 25 per cent longer. The reasons for arbitrarily placing them in different genera, as well as species, have been given above. It is probable that *M. argentinus* was of approximately the size of *M. reigi*, with which direct comparison is impossible at present. I find the dimensions of the type (appressed metatarsals) of *M. argentinus* to be slightly larger than those given by Ameghino: 28.6 in length and 2.4 in (transverse) width at the narrowest point. The minimum anteroposterior diameter is 1.5.

Microtragulus catamarcensis (L. Kraglievich)

Argyrolagus catamarcensis L. Kraglievich, 1931, reprinted in L. Kraglievich, 1940, p. 592. (Not previously figured.)

Type. MACN No. 5529. Parts of both rami of the mandible with left I₁ and P₃-M₄ (poorly preserved), right I₁, and M₁₋₃, and other alveoli and fragments.²

Hypodigm. Type only.

Known range. Araucanian of Catamarca ("los yacimientos araucanenses de Catamarca"). A label with the specimen says, "Andalhualá Catamarca F. Araucana." Andalhualá is evidently named as at or

¹ "Es el más pequeño de los artiodáctilos conocidos, pues su tamaño no excedía al de una pequeña rata. . . . El hueso metatarsiano ó cañón formado por la fusión de los dos metatarsianos 3 y 4, solo tiene 27 mm. de largo y 2 mm. de ancho en su parte media más angosta. . . . Los dos metatarsianos en cuestión . . . están soldados en todo su largo, pero se conserva entra ambos un profundo surco longitudinal en su cara anterior y otro más superficial en la cara posterior. Los metatarsianos laterales 2 y 5 son atrofiados, representados tan sólo por sus extremidades proximales estiliformes, siendo esta parte del metatarsiano 5 soldada con la del metatarsiano 4, pero la del metatarsiano 2 se conservaba independiente. El cuboides, el escafoides y los cuneiformes se conservan independientes, pero contruidos, como también los demás huesos, sobra el mismo tipo del de los Tragulidae."

² In the same vial there is a fragment of bone with a lower molar tooth apparently of *Caroloameghinia mater*, a rare genus and species known only from the Casamayoran of Patagonia. There cannot be any connection between the two specimens.

near the locality where the specimen was found. It is also the type locality for a subdivision of the Araucanian beds, and there is some probability that the specimen came from that stratigraphic subdivision. It is shown, for example, on the correlation chart, pl. IV, of J. L. Kraglievich (1952).

Original diagnosis. No formal proposal or diagnosis was given, but, in the course of a discussion of *Argyrolagus palmeri*, L. Kraglievich gave this name as new,³ with enough description to validate the name under the then existing code of nomenclature; from that discussion I have abstracted such comments as might have been considered distinctive of the species in comparison with *A. palmeri*.

"In the Araucanian deposits of Catamarca, somewhat older than that of Monte Hermoso, I have established the presence of another argyrolagid, which I shall call *Argyrolagus catamarcensis* n. sp., much smaller than *A. palmeri*. The animal is represented by a large part of the mandible (No. 5529, paleontological collection of the National Museum), with the body of both rami, the median incisors and several cheek teeth of one side or the other, of really tiny size but of a structure similar to the genotype species in every respect."⁴ There follows a description not said to be and not in fact distinctive from *A. palmeri*. Then: "Perhaps the anterior accessory groove of the second cheek tooth [M_1] (the first preserved) is a little weaker than in *A. palmeri*. The anteroposterior diameter

of the median incisor scarcely exceeds 1 mm. The maximum height of the rami below the cheek teeth does not reach 5 mm, and the three intermediate cheek teeth [i.e., the second to fourth or M_{1-3}] occupy a space of only 4 mm."⁵

Revised diagnosis. Smaller than *H. reigi*; M_{1-4} 31 per cent longer in type of the latter than in type of *H. catamarcensis*. Lingual groove absent on M_{1-3} . Measurements in Table 1.

Discussion. The brief new diagnosis suffices to distinguish this species from others in which the lower dentition is known. Further details are given in the discussion of anatomy. It is improbable that this name is synonymous with *H. argentinus*. The type metatarsals of the latter are probably too large for *H. catamarcensis*, and there is considerable difference in geological age.

*Microtragulus reigi*⁶, new species

Type. MMMP No. 960-M, part of right mandibular ramus with all teeth. Collected by G. Scaglia at Punta San Andrés, San Andrés Formation.

Hypodigm. The type and the following: MMMP No. 714-S, part of left mandibular ramus with M_{2-4} ; collected by O. Reig in

³ This offhand presentation, buried in a text paragraph, doubtless explains why "*A.*" *catamarcensis* does not figure in the relevant bibliography, Camp and Vanderhoof (1940), which does cite the publication in which the name appeared.

⁴ In fact the structure of these teeth is strikingly different from that of *Argyrolagus palmeri*, as is now shown. That an observer of L. Kraglievich's high caliber thought the structure the same is due to the fact that the outlines of the molars were obscured by matrix, which has subsequently been removed without damage to the specimen.

⁵ "... en los yacimientos araucanenses de Catamarca, algo más antiguos que el de Monte Hermoso, he comprobado la presencia de otro argyrolágido, que denominaré *Argyrolagus catamarcensis* n. sp., mucho más pequeño que *A. palmeri*. El animal está representado por una gran parte de la mandíbula (N° 5529, colecc. paleont. Mus. Nac.), con el cuerpo de ambas ramas, los incisivos medios y varios molares de uno y otro lado, de un tamaño verdaderamente diminuto, pero de una conformación en todo similar a la especie genotipo. . . . Tal vez el surco accesorio anterior del m 2 (primero de los molares conservados) es un poco más débil que en *A. palmeri*. El diámetro anteroposterior del incisivo medio apenas pasa de 1 milímetro; la altura máxima de las ramas debajo de los molares no llega a 5 milímetros y los tres molares intermedios ocupan tan sólo un espacio de 4 milímetros."

⁶ For Dr. Osvaldo Reig whose essential contributions to this study are acknowledged above.

a disgorged food pellet in the Atlantic coastal cliff 300 meters south of the Arroyo Loberia, Vorohué Formation, bed III. MMMP No. 691-S, nearly complete skull, lacking snout; collected by G. Scaglia at foot of cliff 120 meters south of the Bajada de las Palomas, Chapadmalal Formation, probably bed 3 or 4. MMMP No. 661-S, right maxilla with P^3-M^4 ; collected by G. Scaglia 500 meters south of Punta Vorohué, one meter above sea level, Barranca de los Lobos Formation. MMMP No. 395-M, fragments of maxilla and mandible, with limb bones and fragments of several (probably three) individuals, perhaps not all of this species; collected by G. Scaglia in the cliff 550 meters northeast of Arroyo Brusquitas, Barranca de los Lobos Formation, bed I. Some of the skeletal remains, not associated with teeth, listed and described under "anatomy" probably belong to this species, but only specimens with teeth are explicitly placed in the hypodigm.

Known range. Early Pleistocene (Chapadmalal to San Andrés formations) of the Chapadmalal-Miramar region, Buenos Aires Province. More precise localities and horizons of the known specimens given above.

Diagnosis. Larger than *M. catamarcensis*. M_{1-3} with shallow but definite lingual grooves. Measurements in Tables 1 and 2.

Discussion. No metatarsals that could be referred to this species are known from the beds in which the teeth of the hypodigm were found. Comparison with the type of *M. argentinus* is therefore impossible. The two nominal species are of about the same size, although a metatarsal somewhat smaller than the type of *M. argentinus* might be expected in *M. reigi*. The Monte Hermoso and Chapadmalal, *sensu lato*, faunas are largely different. Virtually no species are recorded as common to both, and L. Kraglievich's enumeration (1934) shows only 24.3 per cent of total then known and well-identified genera as present in both, although he indicated that 54.5 per cent of the well-identified genera of the smaller Monte Hermoso

fauna are present in the (unrestricted) Chapadmalal. The specific distinction may well be exaggerated by the tendency to define nominal species as distinct just because the specimens in question are from different beds. Nevertheless, the Monte Hermoso fauna clearly is largely different from that of the Chapadmalal or any known later fauna. Reference of the Chapadmalal-San Andrés specimens to the Monte Hermoso species would go against some probability. A name is needed for these excellent and important specimens, and dubious reference to the earlier species would now be more misleading than reference to a new species, even though the name of the latter could conceivably later prove to be a synonym.

Genus *Argyrolagus* Ameghino

Argyrolagus Ameghino, 1904, vol. 58, p. 255.

Type. *Argyrolagus palmeri* Ameghino.

Referred species. *A. scagliai*, new species, and doubtfully ?*A. parodii* Rusconi.

Known range. Late Pliocene (Monte Hermoso) to early Pleistocene (Chapadmalal), Argentina.

Diagnosis. (Differential from the only other genus now recognized in the family, called *Microtragulus* by the arbitrary usage previously explained.) M_{1-4} strongly and definitely bilobed, with opposite labial and lingual vertical grooves of approximately equal strength; definitely longer than wide; second lobe relatively longer than in *Microtragulus*. M_4 not so markedly unlike M_3 .

Discussion. The characters noted in the diagnosis sharply distinguish these species from those here designated as *Microtragulus catamarcensis* and *M. reigi*. Comparison with the genotype of *Microtragulus*, *M. argentinus*, is possible for *A. scagliai*, but indicates only that the metatarsals of the latter species are longer and stouter than those of the former. As previously explained, it is possible that the type of *M. argentinus* does belong to *Argyrolagus*, in which case *Argyrolagus* is a synonym of

Microtragulus, and the species here called *M. catamarcensis* and *M. reigi* do not belong to that genus. It is, however, at least equally plausible that a real generic distinction simply is not evident in the metatarsals. There are many examples among mammalian genera closely related but generally accepted as distinct in which the generic distinction is not evident in metatarsals or other limb segments. The resemblance does indicate close relationship and shows beyond serious doubt that *Microtragulus* and *Argyrolagus*, whether truly distinct genera or not, do belong in the same family.

Other characteristics of *Argyrolagus*, as here restricted, are given in the section on anatomy.

*Argyrolagus palmeri*⁷ Ameghino

Argyrolagus palmeri Ameghino, 1904, vol. 58, p. 255; Ameghino, 1906, fig. 221; L. Kraglievich, 1931, fig. 2.

Type. Ameghino Collection, presumably in MACN but not seen, part of a left mandibular ramus with I_1 , M_{1-4} , and alveoli of I_2 and P_3 .

Hypodigm. Type only.

Known range. Monte Hermoso Formation at Monte Hermoso, Buenos Aires Province.

Original diagnosis (of genus and species). "Medial incisor narrow, flat on the internal and convex on the external side, as in *Prolagus*; the root of this incisor reaches only as far as below the fifth cheek tooth. The second incisor smaller, elliptical, located posterior to the medial incisor and separated from the following cheek tooth

by a short diastema. The five cheek teeth in continuous series, the first elliptical and the following four composed of two prisms, all very long and with open roots. Horizontal ramus with a very convex ventral border. Length from the anterior part of the medial incisor to the posterior edge of the last cheek tooth 14.5 mm. Length of the space occupied by the five cheek teeth 9 mm."⁸

Revised diagnosis. About the size of *A. scagliai* or slightly smaller. Anterolabial projection of M_1 less pronounced. M_{1-3} narrower relative to length. Talonid of M_4 without posterior projection. Measurements derived from illustrations in Ameghino (1906) and L. Kraglievich (1931) are given in Table 1.

Discussion. Ameghino's original diagnosis or, rather, description was not differential, as there was then nothing to compare with. Even the supposedly related lagomorphs are all so obviously different that a diagnosis against them was unnecessary. Of course it has long since been recognized that this was because the groups are not, in fact, related. Although the specimens here grouped in *Microtragulus* are indeed related to *A. palmeri*, those with known lower dentitions (*M. catamarcensis* and *M. reigi*) are quite distinct, as indicated here by their generic

⁸ "Incisivo interno angosto, plano sobre lado interior y convexo sobre el externo, igual al de *Prolagus*; la base de este incisivo sólo llega hasta debajo de la muela 5. Incisivo segundo más pequeño, elíptico, colocado detrás del incisivo interno y separado de la muela que sigue por una barra corta. Las cinco muelas en serie continua, la primera elíptica y las cuatro siguientes compuestas de dos primas [sic!], todas muy largas y de base abierta. Rama horizontal de borde inferior muy convexo. Longitud de la parte anterior del incisivo interno al borde posterior de la última muela, 14.5mm. Longitud del espacio ocupado por las 5 muelas, 9mm."

Ameghino designated all permanent postcanine teeth in mammals, premolars and molars of other authors, as molars; I therefore translate his "muela" as "cheek tooth." "Primas" is an obvious misprint for "prismas."

⁷ The name was given in honor of the North American mammalogist T. S. Palmer, author of the *Index Generum Mammalium*, a work now sometimes maligned but still extremely useful and irreplaceable; indeed even now, as Ameghino wrote in 1904, "The most complete and perfect compilation of its sort ever written." It had just been issued when Ameghino wrote those words in a footnote to his description of this genus and species.

separation. *A. scagliai*, new here, is much closer to *A. palmeri*, but the characters indicated in the diagnosis adequately indicate specific distinction. The two are of definitely, although not greatly, different ages.

I have not seen the actual specimen, but the descriptions by Ameghino and especially by L. Kraglievich are detailed, and they agree well, as do their figures, three of which are given by Ameghino and two by L. Kraglievich. As shown in Table 1, measurements made on these figures (all of which are $\times 2$), although differing by as much as 0.4 mm in extreme cases, are in sufficiently close agreement to be trusted as approximate, at least, when averaged.

Argyrolagus scagliai,⁹ new species

Type. MMMP No. 785-S, nearly complete skull, left ramus of mandible, pelvis and sacrum, right and left femora, right and left tibiae and fibulae, right and left metatarsals, partial right and left tarsi, part of scapula, partial right and left humeri, vertebrae, and various fragments; collected by G. Scaglia, 200 meters north of the Bajada de los Lobos, Chapadmalal Formation, bed 9.

Hypodigm. Type and the following: MMMP No. 741-M, part of right mandibular ramus with all teeth; from the Bajada las Palomas, Chapadmalal Formation, bed 9. MMMP No. 802-M, most of skull, lacking snout; from Punta Plataforma, Chapadmalal Formation. MMMP No. 281-S, partial left side of skull; collected by G. Scaglia 100 meters south of the Bajada de la Barranca de los Lobos, Chapadmalal Formation, bed 9. MMMP No. 973-M, most of palatal and adjacent facial parts of skull with all teeth except right I^1 ; collected by G. Scaglia at Vivero, Arroyo Lobería, Chapadmalal Formation, bed 8. MMMP No. 974-M, part of left ramus with P_3-M_2 ; collected by G. Scaglia on the south side

of Arroyo Brusquitas, Chapadmalal Formation, bed 9. Some of the skeletal parts mentioned in the section on anatomy may also belong to this species, but they are not formally included in the hypodigm.

Known range. Chapadmalal Formation, early Pleistocene, of the Chapadmalal-Miramar region, Buenos Aires Province. Details given above. (By what is probably coincidence, all the identified specimens of exactly known level are from beds 8 and 9 of the Chapadmalal, relatively high levels in that formation.)

Diagnosis. About the size of *A. palmeri* or slightly larger. Pronounced anterolabial projection on M_1 . M_{1-3} relatively wide (more than in *A. palmeri*, less than in *Microtragulus*). M_4 talonid relatively complex, with posterior projection.

Discussion. This, now much the best-known species of the family, is described in detail in the section on anatomy.

?*Argyrolagus parodii* Rusconi

Argyrolagus Parodii Rusconi, 1933, p. 245, figs. 1 and 10; 1936, figs. 6b, 9, 10, and 12.

Type. Part of a left mandibular ramus with M_{3-4} . This was collected by Lorenzo W. Parodi, apparently on his own and not for a museum or other institution. He turned the specimen over to Carlos Rusconi, who has informed me (letter of 24 October 1967) that the specimen "is in my possession (in my house), but unfortunately someone has broken it and it is in small bits. I do not know whether it can be reconstructed."¹⁰ Evidently comparisons are now impossible, and Sr. Rusconi did not think it worth while to forward the remaining fragment or fragments for comparison.

¹⁰ "... se halla en mi poder (in my house) [parenthetical expression English in the original]. Pero, desgraciadamente alguna persona me la ha roto y se encuentra en pequeños trozos. Ignoro si podría ser reconstruida." Rusconi then adds in English, "(This mandibular fragment in [is] broken or destroyed but [I] preserve some fragment.)"

⁹ For Galileo Scaglia, who collected many of the specimens here described, who made them all available, and who supplied the data on localities and levels.

TABLE 1. MEASUREMENTS OF LOWER TEETH OF ARGYROLAGIDAE

	M_1		M_2		M_3		M_4		LM_{1-4}	LM_3/LM_4	LM_3/WM_3
	L	W	L	W	L	W	L	W			
<i>Microtragulus</i>											
<i>M. catamarcensis</i> , type	1.2	0.8	1.2	1.2	1.2	1.0	1.1	0.7	4.8	1.09	1.20
<i>M. reigi</i> , type	1.6	1.3	1.6	1.4	1.7	1.6	1.5	1.1	6.3	1.11	1.06
MMMP No. 714-S	—	—	1.5	1.5	1.5	1.4	1.4	0.9	—	1.07	1.07
<i>Argyrolagus</i>											
<i>A. palmeri</i> , type											
From Ameghino, 1906,											
Fig. 221a	1.8	1.1	1.9	1.3	2.0	1.3	1.7	1.2	7.5	1.18	1.54
Fig. 221e	1.9	—	1.9	—	2.1	—	1.9	—	7.6	1.10	—
Fig. 221o	2.0	—	2.1	—	2.0	—	2.0	—	7.8	1.00	—
From Kraglievich, 1931											
Fig. 2, upper	1.7	1.1	1.9	1.3	2.0	1.3	2.0	1.1	7.7 ^a	1.00	1.54
Fig. 2, lower	1.6	—	2.2	—	2.4	—	2.0	—	7.7	1.20	—
Mean of five preceding ^b	1.8	1.1	2.0	1.3	2.1	1.3	1.9	1.15	7.66	1.10	1.62
<i>A. scagliai</i> , type	1.7	1.4	2.0	1.7	2.0	1.6	2.2	1.2	8.5	0.91	1.25
MMMP No. 741-M	2.1	1.9	2.3	1.8	2.1	1.8	2.2	1.3	8.4	0.95	1.17
MMMP No. 974-M	2.0	1.8	2.3	2.0	—	—	—	—	—	—	—
<i>?A. parodii</i> , type											
Rusconi, 1933, text	—	—	—	—	1.9	—	1.3	—	—	1.46	—
Rusconi, 1933, fig. 1a	—	—	—	—	1.8	1.6	1.6	1.2	—	1.12	1.12
Rusconi, 1936, fig. 12	—	—	—	—	1.6	1.4	—	—	—	—	1.14

^a Kraglievich gives 7.5 in the text.^b This is a mean of the five sets of measurements derived from different illustrations of the same specimen; it is not a mean of five specimens or five independent measurements.*Hypodigm.* Type only.

Known range. This specimen was found and described before J. L. Kraglievich and his associates had restricted the Chapadmalal Formation and given new names to overlying beds. It was published (Rusconi, 1933) as from "Miramar, province of Buenos Aires; *Chapadmalense* beds, Middle Pliocene." In reply to my enquiry as to whether any more precise data are available, Rusconi kindly replied, "This type specimen, according to friend Parodi, was found by him in the Chapadmalalan? terrain, between the localities Las Brusquitas and Vuelta Mala, on 30 January 1932. Nevertheless it is possible that the exact level of the fossil may have been between the Post-Chapadmalalan and the Ensenadan. I do not know personally the exact spot from which said specimen

comes."¹¹ Vuelta Mala is not indicated on maps available to me, but there is an Arroyo las Brusquitas approximately 5.7 kilometers northeast of the center of the town of Miramar, and J. L. Kraglievich (1952, plates I and II) indicates a Barranca Parodi a short distance southwest of the mouth of that arroyo. The specimen in question doubtless came from that general region. According to J. L. Kraglievich, the only beds exposed within several kilometers of there are the Chapadmalal,

¹¹ "Esta pieza tipo, según el amigo Parodi, la encontró en terreno chapadmalense?, entre las localidades de las Brusquitas y Vuelta Mala, Enero 30 de 1932. Sin embargo puede ser que el nivel justo del fósil haya sido entre el Post-chapadmalense y el Ensenadense. Yo, personalmente, no conozco el lugar exacto de donde procede dicha pieza."

Vorohué, and Lobería formations. The Lobería is latest Pleistocene or Recent and it is highly improbable that the specimen came from it. The specimen almost certainly came from the Chapadmalal, *sensu stricto*, or from the immediately succeeding and hardly appreciably later Vorohué. Its age according to most present usage is therefore early Pleistocene.

Original diagnosis. A separate, formal diagnosis was not given; I have extracted from the extended description specifications of characters evidently considered diagnostic. The original publication is in English, translated by Violeta Lelong from the author's Spanish manuscript.

"Ascending ramus lower than that of *Argyrolagus palmeri*, but somewhat larger than that of the *A. catamarcensis* Kragl. . . . Between M_3 [i.e., the last cheek tooth, M_5 of Ameghino and L. Kraglievich, M_4 of usual notation for marsupials] and the coronoid crest there is an excavated surface that is placed in an oblique direction and in whose bottom there is a vertically descending hole that communicates with the posterior dental foramen. . . . This canal apparently does not exist in *A. palmeri*. . . . The anterior margin of the coronoid crest of *A. palmeri* is inclined obliquely downward. It describes a feeble curve and terminates at the level of the penultimate molar. The corresponding margin of *A. parodii*, on the contrary, ends in a strong, bony edge, bent downward nearly at a right angle, and behind it there appears an irregular and rather characteristic depression. . . . The inferior mandibular edge in the new species, principally from the level of the penultimate molar backwards, is straighter than it is in *A. palmeri*. There is some difference between the two hinder molars, but the most important is the slightly greater thickness of M_3 [M_4] as compared with the penultimate molar. In *A. palmeri* these teeth are of nearly equal size."

Tentative revised diagnosis. M_3 about the size of *A. palmeri* and *A. scagliai*, but

relatively wider, talonid lobe shorter, buccal and lingual grooves opposite, subequal. M_4 with second lobe more distinct, less narrowed than in *Microtragulus catamarcensis* but more narrowed than in *Argyrolagus palmeri* and *scagliai*.

Discussion. As the type has been virtually if not literally destroyed and no other specimens surely conspecific are known, judgment must now be based on Rusconi's description and figures and on two unpublished photographs, one in labial and the other in lingual view, kindly sent to me by Rusconi for this study. These photographs, scale not indicated but probably about $\times 1\frac{1}{2}$, do not agree in detail with Rusconi's published figures, and when they were taken the specimen apparently had already suffered some breakage although it had not yet been reduced to fragments.

The three views in Rusconi (1933, fig. 1) are marked " $\times 2$ " but according to Rusconi's measurements (p. 250), that is approximately correct for figure 1a, only. The scale of 1b and 1c (assuming the table of measurements to be nearly correct) is approximately $\times 1\frac{1}{2}$. Rusconi gives 1.9 and 1.3 as the lengths of M_3 and M_4 (his " M_2 " and " M_3 ") respectively. If these figures are correct, M_3 is near the size of *Argyrolagus palmeri* and *A. scagliai* but M_4 is at least as small as in *Microtragulus reigi*. The ratio LM_3/LM_4 on these figures is 1.46, much larger than in any other known specimen of this family, and that may be a distinction of the species. However, if we accept figure 1a as being $\times 2$, the two lengths measured thereon are 1.8 and 1.6, the ratio 1.12, which is within the range for both *M. reigi* and *A. palmeri*. (See Table 1.)

The crown view, figure 1a, in Rusconi's first paper (1933) seems to differ considerably from that, figure 12, in his later discussion (1936). If the former is correct, this tooth would appear to have a deeper lingual groove than any other M_3 known in the family and to have this posterior to

the labial groove, not opposite the latter. Such a structure would be highly distinctive. However, the later figure is clearer and is also drawn to a larger and apparently more accurate scale. I have therefore assumed it to be correct, an assumption that cannot be checked until other specimens of this species are found. On this assumption, M_3 resembles *Argyrolagus* in having subequal labial and lingual grooves but *Microtragulus* in having a short talonid. The distinction and narrowing of the talonid of M_4 is approximately intermediate between those genera, in species more definitely referred to them. It is thus quite unlikely that ?*A. parodii* is synonymous with any other, earlier or later, specific name. Generic reference is uncertain, but the later figure of M_3 (Rusconi, 1936, fig. 12) is perhaps nearer to *Argyrolagus* than to *Microtragulus*.

The other characters given by Rusconi are not distinctive. The statement that the ascending ramus is lower in his type is puzzling, because the height of that part was not determinable in that specimen or any other of this family available for comparison. The vertical canal posterior to the molars is present in all specimens of the family in which this region is preserved. L. Kraglievich (1931) had already noted its presence in *A. palmeri*. The ridge and depression on the buccal side of the ramus are also normal for the family, but they vary in degree of prominence. In Rusconi's type they do seem to be more prominent than in some specimens, yet not uniquely so. This might be a character of sex or of individual age. The apparent difference in curvature of the ventral border of the ramus, slight in any case, is largely if not wholly an effect of the way in which the specimen is broken and dependent on what was accepted as a normal horizontal. The latter is also the cause of the supposed peculiarity, discussed by Rusconi at length and subject of extended pictorial comparisons (Rusconi, 1933, figs. 2–11) that the condyle is below the level of the

alveolar border. The error was natural at the time, but now that more complete jaws are known it is seen that the border is rising posteriorly under M_{3-4} and there is not indicative of a true horizontal. When the whole alveolar border is taken into consideration, the condyle is above its level. This effect can be seen in Rusconi's figure (1933, fig. 4) of the mandible of *Paraepanorthus* (a caenolestid). If the line "X" indicating the level of the alveolar border in *Paraepanorthus* were drawn from M_{3-4} only, the condyle would be well below it, not above it as (correctly) shown. It follows that Rusconi was also mistaken in deducing that the glenoid cavity of the skull of his specimen of *Argyrolagus* must have been beyond (i.e., below) the level of the triturating surface of the upper molars. (See section on anatomy later in this study.)

ANATOMY

Dentition. The following description of the dentition is based primarily on *Argyrolagus scagliai* and especially on the type of that species, MMMP No. 785-S. Notable divergences from that species and specimen are noted. Striking differences believed to be of taxonomic importance have been incorporated in preceding diagnoses of taxa.

Each side of each jaw, upper and lower, has two gliriform-incisiform anterior teeth. Those in the upper jaw are in the premaxilla and are therefore incisors. Those in the lower jaw are also almost surely incisors. Their homologies among the more numerous ancestral incisors are not surely determinable, but the more anterior are nearly medial in position, and the next follow without diastemata. It is therefore plausible, at least, that these teeth are I_{1-2}^{1-2} , and in any case they can be so designated for purposes of description. They are followed in each jaw by a prominent diastema and then by five cheek teeth in closed sequence. The first of these, although not strictly styliiform

as previously described (for the lower dentition), are distinctly unlike those following and are simpler in structure. The other four teeth, with some differences among themselves, form a graded, molariform series. The available specimens show no evidence of tooth replacement. The homologies of these cheek teeth with the longer ancestral sequence are, again, not strictly determinable, but it is plausible that they are homologous with the teeth usually designated $P_3^3 M_{1-4}^{1-4}$ in marsupials.¹² The conventional dental formula is therefore adopted as $\frac{2.0.1.4}{2.0.1.4}$ and provisionally homologized as $I_{1-2}^{1-2} P_3^3 M_{1-4}^{1-4}$. Although this is convenient for purposes of description, the homologies of I_{1-2}^{1-2} in this family are uncertain with respect to other marsupials, and the teeth almost always designated P_3^3 in marsupials may be incorrectly numbered by ancestral homologies.

As far as determinable, all teeth are completely hypselodont, continuously growing. In MMMP No. 661-S postmortem erosion has laid open the dorsal ends of the crypts of the upper cheek teeth. Although all of these have erupted and are worn, the pulp cavities are wide open and there is no sign of the formation of roots. The corono-basal length of M^2 is 7.3, which is 4.3 times the anteroposterior length of the crown. The corono-basal length of the other cheek teeth is somewhat less. These teeth certainly continued to grow for a long time, and probably did so continuously throughout the life of the animal. No specimen, as now prepared, positively demonstrates this for the incisors, but it is highly probable for them as well.

I^1 is a large tooth, somewhat curved (convex anteriorly) in the corono-basal direction. The mouths of the alveoli of left and right I^1 are slightly separated, but the curvature and implantation of the teeth are such that their working faces are in

contact medially. Each tooth is triangular in cross section, with each of the three sides slightly curved. Longest is the flattened labial face. The medial point is the apex of the triangle. The short side is postero-labial (or distal) and abuts against I^2 . The exposed part of I^1 is recumbent and works against the end of strongly procumbent I_1 . On both I^1 and I^2 the labial face is well enameled, but enamel is thin or possibly absent on the lingual face. I^2 , somewhat larger than I^1 , is slightly procumbent. Its anterior (or mesial) tip lies against the tip of I^1 . The cross section is that of a long, thin oval or tear drop, the broader end anterior, the thin, following (posterior, distal) end almost angular.

Nominal P^3 is a small, comparatively simple tooth, somewhat recumbent so that it is tightly appressed against the middle of the anterior (mesial) face of M^1 , immediately lingual to its parastylar lobe or projection. The cross section of P^3 is long subovate or subtriangular, the blunt end posterior.

In *A. scagliai* M^1 is abruptly larger than P^3 ; M^2 is still larger, M^3 about the size of M^1 , and M^4 slightly smaller than M^{1-3} but still larger than P^3 . In *M. reigi* there is little difference in size in M^{1-3} but M^4 is markedly smaller, relatively more so than in *A. scagliai*. These differences are evident in Table 2. In both genera and species M^{1-3} are somewhat flattened on all four of the more or less vertical faces, and hence are subquadrate. Anterior and posterior (mesial and distal) faces are roughly equal on M^1 , but on M^{2-3} the posterior face is progressively shorter, and on M^4 it is so short that the cross section or coronal outline of that tooth is almost triangular. Lingual faces are simply and gently rounded. Buccal faces are flattened and have very faint vertical grooves or concavities that come to correspond in course of wear with notches between points that develop on the enamel of the buccal wall. As viewed from the buccal side, M^1 develops a low, small anterior and a higher, broader pos-

¹² At this point it is assumed that these animals are marsupials. The evidence is given in the course of the present section on anatomy.

TABLE 2. MEASUREMENTS OF UPPER TEETH OF ARGYROLAGIDAE

	M ¹		M ²		M ³		M ⁴		LM ¹⁻⁴	LM ² /LM ⁴
	L	W	L	W	L	W	L	W		
<i>Microtragulus reigi</i>										
MMMP No. 691-S	1.5	1.3	1.4	1.4	1.4	1.2	0.8	0.8	5.2	1.75
MMMP No. 661-S	1.6	1.6	1.7	1.6	1.6	1.4	0.9	1.1	5.9	1.78
MMMP No. 395-M	1.7	1.6	ca. 1½	ca. 1½	ca. 1½	ca. 1½	—	—	—	—
Means	1.60	1.50	ca. 1.5	ca. 1.5	ca. 1.5	ca. 1.4	0.85	0.95	5.55	1.76
<i>Argyrolagus scagliai</i>										
MMMP No. 785-S	1.7	1.8	2.2	1.7	2.2	1.8	ca. 2	1.3	7.9	1.1
MMMP No. 802-M	1.8	1.6	1.9	1.7	1.8	1.5	1.5	1.1	7.0	1.20
MMMP No. 281-S	2.0	1.7	—	—	—	—	ca. 1½	1.3	7.6	—
MMMP No. 973-M	2.1	1.7	2.0	1.9	1.7	1.7	1.4	1.4	7.2	1.21
Means	1.90	1.70	2.03	1.77	1.90	1.67	ca. 1.6	1.28	7.42	ca. 1.17

terior point. M²⁻³ have two points closer to each other and separated by a low prominent notch, one point medial on the buccal face and the other, slightly higher, posterior to it. M⁴ tends to develop a single, approximately medial point.

As seen in crown view or section, M¹, but not the other molars, has anterobuccal or nominally parastylar (possibly paraconal?) lobe or projection. When little worn (e.g., M⁴ of MMMP No. 785-S, *M. reigi*, or M¹⁻⁴ of MMMP No. 691-S, *A. scagliai*), the molar crowns have a shallow, apparently quite simple basin, with a papillate rim, the buccal side considerably elevated above the lingual side. The sharp projection of the buccal side is maintained with wear and bears an interesting resemblance to that of *Caenolestes*. The teeth are thickly enameled on all sides. In some specimens there may be a thin coating of cement, especially on the lingual side, but without examination of thin sections this is not definitely established.

As may be seen in Table 2, M²⁻⁴ and, to less extent, M¹ tend to be decidedly longer than wide in *A. scagliai*, but M¹⁻⁴ are more nearly equidimensional in *M. reigi*. Except for the noted differences in size and proportions, no marked generic or specific distinctions are observed in the upper dentitions.

The two lower incisors, nearly parallel, are procumbent and strongly curved, convex anteroventrally. The alveoli are separated by bone, but the working apices are appressed. I₁ is distinctly larger than I₂. In section the labial face of I₁ is almost simply and slightly convex. The mesial end is bluntly pointed, and the lingual side is gently concave. The short distal side is also slightly concave. The cross section of I₂ is simpler, the labial face definitely and lingual face slightly convex. The greatest transverse width tends to be somewhat anterior, and in some instances there may be a flattening or very slight concavity posterior to this. In some specimens, e.g., MMMP No. 960-M, *M. reigi*, the incisors are surrounded by enamel, and in others, e.g., MMMP No. 714-S, also *M. reigi*, enamel is present only on the labial faces. This is probably an individual age difference, with the latter condition in older individuals. Wear on these teeth is quite unlike that in rodents. The wear surface on I₁ is almost horizontal, slightly concave longitudinally. On I₂ an almost flat surface slopes mesio-lingual to labio-distally.

The lower diastema is short, about equal to or less than the longitudinal dimension of the alveolus of I₂.

In the following paragraphs, the lower cheek teeth of *Argyrolagus scagliai* are first

described, and distinctions of the other known species are then detailed one by one.

The cross section of nominal P_3 is more or less oval, the longer transverse diameter posterior, but also subtriangular from moderate, separate flattening of the buccal, posterior, and lingual faces.

M_{1-4} of *Argyrolagus scagliai* are strongly bilobed by the presence of a deep, sharp, vertical groove (a flexid in rodent terminology) on each of the buccal and lingual faces. These are directly opposite one another and not offset as is usual in rodents and some other groups. The anterior lobe, undoubtedly derived from an ancestral trigonid, is decidedly longer than the posterior (talonid) on M_{1-4} . On M_1 the anterior lobe is narrower, but anterior and posterior are of about equal width on M_{2-4} . Lengths and widths of the anterior lobes are roughly equal. On M_{1-3} the posterior lobes are about twice as wide as long, but on M_4 these dimensions are nearly equal. The anterior lobes are all somewhat but irregularly quadrate. On all, the most anterior point is anterobuccal. On M_1 this forms a slightly lobate projection, but on M_{2-4} this point is only angulate, the angle slightly less than 90° . On the buccal face of M_1 there is a vertical convexity posterior to the lobule, but on M_{2-4} this face is merely flattened. On all, it has an angulate posterobuccal corner, the angle here greater than 90° . The lingual faces of M_{1-4} also have anterior and posterior angles, both greater than 90° , and between the angles all have shallow vertical grooves or concavities. On M_1 the general direction of this face (in horizontal section) is oblique, posterolingual to anterobuccally. The obliquity is progressively less on M_{2-4} and the face is almost fully anteroposterior on M_4 . The posterior lobes on M_{1-3} are transversely elliptical; that of M_4 is almost circular but has a posteromedial projection. On young specimens, P_3 - M_4 are nearly or quite surrounded by enamel on all faces. On older specimens, the enamel on the lingual face

of P_4 is thin or absent. Enamel persists on the lingual faces of M_{1-4} but becomes thin or absent, perhaps from wear, where those teeth are appressed against their neighbors. Old individuals have what may be a thin layer of cement on the buccal faces of M_{1-4} , but one cannot be certain of this without histological study.

P_3 is absent in the type and only known specimen of *Argyrolagus palmeri*, but its alveolus indicates an elongate-oval or subtriangular tooth, much as in *A. scagliai*, but perhaps relatively longer and narrower. M_{1-3} are definitely more elongate in *A. palmeri*; M_4 is shorter relative to M_3 . (See Table 1.) The available figures (Ameghino, 1906, fig. 221; L. Kraglievich, 1931, fig. 2) are not wholly satisfactory as to structural details, but they indicate that on M_1 the trigonid is less triangular in *A. palmeri*, without a distinct anterobuccal projection or buccal concavity on the trigonid, and that on M_4 the talonid is shorter, without a posteromedial projection.

In the only known specimen of *Microtragulus catamarcensis*, P_3 is rounded-triangular, about as in *M. reigi*. M_1 is subtriangular, with an acute anterobuccal apex and a flattened buccal face which is plane or very slightly concave on the trigonid, and a relatively posterior flexid entering to about one-fourth the transverse width of the tooth and marking off a very short talonid equal in width to the widest part of the trigonid. The posterior face is nearly flat, meeting the buccal face at a definite angle of about 90° . It curves into the lingual-anterior face, which is a single curved convex surface from posterolingual to anterobuccal, without any concavity or flexid. M_2 differs in being markedly wider, with the anterobuccal angle less acute. M_3 is intermediate between M_1 and M_2 in width but of about equal length. Anterior and lingual faces are somewhat flattened and meet at a somewhat rounded angle, rather than forming a single curve. There is a slight vertical posterolingual concavity, not definite enough or deep enough to be

called a flexid. There is also a vertical concavity on the posterior face. M_4 is elongate oval or almost teardrop in shape, with a rounded trigonid and a much shorter, narrower, subtriangular talonid set off from the trigonid by shallow, rather obscure vertical grooves. All of the molars are quite distinct from those of *Argyrolagus palmeri* or *scagliai*, and that is the reason for confidently referring them to different genera even though the designation of this second genus as *Microtragulus* is uncertain.

The lower cheek teeth of *Microtragulus reigi* are best represented by the type, MMMP No. 960-M, but two other specimens show no marked differences. P_3 , present in the type only, is almost circular in cross section, a slightly curved cylinder. M_1 resembles that of *M. catamarcensis*, but the buccal concavity of the trigonid is more distinct, the posterobuccal lobe (or buccal side of the talonid) projects more, and the posterolingual surface is somewhat flattened but not concave or grooved. On M_2 and M_3 the trigonids are more triangular than in *M. catamarcensis*, and there is a shallow but distinct posterolabial groove or rudimentary flexid on both these teeth, directly internal (labial) to the more developed buccal flexid. M_4 has the same great disparity in size between trigonid and talonid as in *M. catamarcensis*, but the two are more distinctly separated and the trigonid is subtriangular, apex forward, rather than circular. As this tooth is poorly preserved in the only specimen of *M. catamarcensis*, the difference may not have been quite as marked as it seems.

For reasons previously stated, knowledge of the dental characters of ?*Argyrolagus parodii* is unsatisfactory. What is known of M_3 and M_4 in that species is sufficiently discussed in the preceding taxonomic section of this paper.

Mandible. No nearly complete mandible is known, but parts of the horizontal ramus, at least, are known in both genera and all named species except *Microtragulus argentinus*. As for the dentition, description will

be based primarily on *Argyrolagus scagliai*, and additional or different features in other species will be noted. In descriptions of mandible, skull, and skeleton, occasional comparison will be made with *Caenolestes*. This is a convenience for clarity of description, and of other known South American marsupials, caenolestids are indeed most nearly similar, although, as will later be shown, there is probably no special relationship.

The horizontal ramus is short and deep, the ventral border strongly convex in outline (as seen laterally), and the alveolar border distinctly but less strongly concave. Depth increases from the anterior end to the level of M_4 . The two rami are completely separate, even in old animals, and meet on unfused, nearly plane symphyseal surfaces, oval and elongate anterodorsal-posteroventrally. The posterior end of the symphysis is beneath the posterior end of M_1 or anterior end of M_2 but is not clearly distinct from the free lingual surface of the ramus. In MMMP No. 960-M, *Microtragulus reigi*, apparently a rather young but not juvenile individual, symphyseal contact at the posterior parts of the surfaces seems to have been slight and even incomplete.

In MMMP No. 741-M, *A. scagliai*, there is a single mental foramen between the alveoli of I_1 and I_2 and vertically below P_3 . The buccal surface of the ramus posterior to this has scattered smaller foramina or punctations of varying size. The most anterior of these, below M_1 , is largest, although it is smaller than the indicated mental foramen. It could be considered as a second mental foramen. The lingual surface of the ramus in this specimen is also punctate on the ventral half or a bit more, posterior to the symphysis. MMMP No. 960-M, *M. reigi*, is similarly punctate and has two distinct mental foramina of nearly equal size beneath P_3 and between P_3 and M_1 . Other specimens do not clearly show these characters. Both Ameghino's (1906) and Kraglievich's (1931) figures

of the type of *A. palmeri* indicate no mental foramen, although one must have been present.

Only the root or base of the coronoid process or ascending ramus is preserved in known specimens. It arises from a crest that begins on the buccal face of the horizontal ramus about midway (vertically) between ventral and alveolar borders and beneath the anterior end of M_4 . It is quite definite from the beginning in MMMP No. 741-M, *A. scagliai*, somewhat less so in MMMP No. 785-S, same species, and still less in two specimens of *M. reigi* (MMMP Nos. 960-M and 714-S). It is prominent in the type of ?*A. parodii*, although apparently not ending so abruptly anteroventrally. Rusconi (1933) considered this a taxonomic distinction, which is possible, although it seems more probable that it is an individual, sexual, or size difference (or two or all of these). Continuing to rise, this crest becomes a prominent lamina posterobuccal to M_4 and then rises upward in the free coronoid process, broken away in all known specimens and of unknown size and shape but clearly short antero-posteriorly and probably low vertically. Between the lamina and the continuation of the alveolar border posterior to M_4 there is a hollow, and in this in all specimens with this part are indications of a foramen evidently communicating with the dental canal. Although I find no previous mention of it in the literature, it is interesting that what is clearly a homologue of this foramen, although small and somewhat variable, occurs in recent caenolestids.

The angle is preserved in MMMP No. 785-S, *A. scagliai*, and was also present in the now destroyed type of ?*A. parodii*, although not perfectly in either case. It evidently was broad, fully inflected, and excavated or forming a large hollow dorso-buccally. On the opposite (lingual) side of this region is a well-developed flange below the strong, concave masseteric fossa, in which there is a small masseteric foramen.

The condylar process and condyle are also present in MMMP No. 785-S, but breaks between these and the horizontal ramus make their precise relationships uncertain. These relationships were apparently better preserved in the type of ?*A. parodii*. The structure in this region in both (doubtful) genera seems to have been essentially the same and was unique. The condyle is far posterior to the short coronoid process. The surface below and anterior to it is broad, nearly flat on the medial side (above the angle), but excavated and with an everted ventral flange on the lateral side, an arrangement slightly developed in *Caenolestes* and well developed in some diprotodonts, e.g., *Phalanger*, in all of which, however, the posterior projection of the condyle is much less. The articular surface of the condyle is directed dorsally, is irregularly oval in shape but about as broad as long, and is almost flat. These characters are *Caenolestes*-like and quite unlike *Phalanger*. As previously pointed out, Rusconi's belief that the condyle in ?*A. parodii* was below the alveolar level was due to an orientation of the jaw confused by its fragmentary nature in his specimen. In fact, the condyle is distinctly above the alveolar level, but it is lower than in most other marsupials. In this respect the argyrolagids are surprisingly more like *Dasyuroidea* than recent *Caenolestoides* or most *Phalangeroides*. However, the level of the condyle is much as in Rusconi's figure (1933, fig. 4) of the extinct caenolestid *Paraepanorthus*.¹³ It is not so surprising that the condylar level is similar to that in jerboas, which are convergent to argyrolagids in many respects.

Skull. The following specimens include significant parts of the skull:

Argyrolagus scagliai. MMMP No. 785-S, nearly complete skull. MMMP No.

¹³ I consider *Paraepanorthus* as a synonym of *Palaeotheres*. I have not seen a specimen with the condyle preserved and have not checked the possibility of post mortem distortion.

S02-M, cranium and region of cheek teeth. MMMP No. 281-S, left premaxilla, zygoma, and adjacent parts of maxilla and ear region.

Microtragulus reigi. MMMP No. 691-S, most of skull. MMMP No. 661-S, most of right maxilla.

As before, description will be based primarily on *Argyrolagus scagliai*, and especially on MMMP No. 785-S, but details will be added from the other specimens listed and differences will be noted.

The habitus of the skull is highly characteristic and very striking, even at first glance. It is extremely different from that of any other known marsupials but has considerable functional resemblances to some placental rodents, especially Dipodomysinae (in the family Heteromyidae) and Dipodidae. These resemblances are clearly convergent among animals not related beyond the subclass level (Theria). They do not extend to details, and there are also major characters that are nonconvergent. Convergence and function will be further discussed in a later section.

The most striking over-all characters are: the long, slender snout protruding far in advance of the incisors; the enormous orbits and broad interorbital region; the posterior position of the orbit and apparent absence of a temporal fossa; the short, globular cranium; the auditory porus opening posteriorly as well as laterally; the large foramen magnum opening rather ventrally; and the enormous palatal vacuities.

The long snout projects well anterior to the incisors. It retains about the same narrow width but becomes shallower anteriorly. The lower part is formed by the premaxillae, which here meet so that the tube is closed, and the upper part is formed by the nasals. Sutures are unfused in what appear to be fully adult individuals. The narial aperture is imperfect in both specimens retaining the snout (MMMP Nos. 281-S and 691-S) but evidently was undivided, anterior, opening somewhat anteroventrally. I know of no other animals

with such a structure. As close an approach as any is perhaps that of *Dipodomys*, which has a bony projection anterior to the incisors, but this is relatively short and is formed by the nasals only, being open ventrally. The snout of *Caenolestes* is also elongated, but in an entirely different way: it is the anterior part of the palate that is elongated, and there is no projection beyond the incisors. The anterior part of the palate in Argyrolagidae is, indeed, relatively much shorter than in Caenolestidae. The prepalatal projection of the bony snout must, of course, indicate a long, slender nose, but does not indicate a flexible proboscis. *Macroscelides*, which has such a proboscis, has no prepalatal bony projection, and *Dipodomys*, which has such a projection (although short), has no proboscis. It is interesting that another fossil South American marsupial, *Necrolestes*,¹⁴ also has a peculiar pre-incisor prolongation of the bony snout. In other respects, however, this feature is so different in the two groups that it can hardly be considered as convergent and clearly is not homologous.

The premaxillo-maxillary suture rises vertically from the alveolar margin for almost the whole depth of the face, and at the dorsal extreme of the premaxilla there is a short, sharply pointed posterior projection between the maxilla and the nasal. The incisive foramina are large, short, and broad relative to those of *Caenolestes*, in keeping with the fact that this region of the palate is relatively much shorter and somewhat broader. The premaxillo-maxillary sutures on the palate are not entirely clear but seem to have been about as in *Caenolestes* or indeed most marsupials, with the premaxilla forming the antero-lateral part of the rim of each foramen, rather more of that rim than in *Caenolestes*, and the premaxillae together forming most

¹⁴ This genus was long considered an insectivore and has also been referred to the Edentata, but Patterson (1958) has produced convincing evidence that it is a marsupial. See his paper, and its references, for description.

of the medial bar between the foramina with a shorter maxillary extension forming the posterior part.

Posterior to the incisive foramina, there is a short transverse bar formed by the maxillae, and this is followed from the level of the anterior end of P^3 to the posterior edge of the palate, posterior to M^4 , by enormous posterior palatal vacuities. These extend laterally to the alveolar margin, so that there is no bony palate at all medial to the cheek teeth. On the specimens including this region there is no medial bar between the posterior vacuities, as preserved, but this may have occurred and been broken away. If so, it must have been very slender. The posterior border of the palate is also broken in all specimens, but there are indications that it was a slender transverse bar, doubtless formed by the palatine bone although the maxillo-palatine suture is not clear, with a palatal ridge, lateral nodular processes, and a posterolateral foramen on each side, as in *Caenolestes* and many other marsupials.

The fenestration of the bony palate is great, even for a marsupial. The fenestration is also extensive in Recent caenolestids, but less than in argyrolagids. Some other South American marsupials, including some caenolestoids and all borhyaenoids, exhibit an opposite trend, with the fenestration reduced or even lost entirely (see Sinclair, 1906; Paula Couto, 1952).

The maxillo-frontal suture is not perfectly clear in any of the specimens, but in MMMP No. 802-M, it seems to run obliquely anteromedial-posterolaterally from the contact of the maxilla with the posterior expansion of the nasals to the anterior part of the dorsal rim of the orbit. On the facial part of the maxilla, a single small infra-orbital foramen occurs almost halfway, vertically, from the alveolar rim to the dorsal surface of the face above the anterior edge of P^3 . This point is about halfway from the anterior rim of the orbit to the tip of the snout, despite the fact that the snout is so exceptionally long.

It is a concomitant of the strange orbital structure, absolutely unique, as far as I know, and further described below, that although the infraorbital foramen is thus unusually anterior to the orbital aperture, the bony canal leading to it is very short, indeed practically absent. This is best seen in MMMP No. 661-S, *M. reigi*, which is a maxilla broken in such a way as to show both external and internal relationships of the infraorbital foramen. The foramen is between the long intra-alveolar part of P^3 , which curves anterodorsally, and that of M^4 , which is nearly vertical and divergent from that of P^3 . (These parts of M^{1-4} are nearly parallel and close to each other.) The foramen does not lead to a canal but opens directly into the large space open in the bony skull, because of the palatal vacuities, and above the soft palate in life. Hence there are signs of a groove, indicating the probable presence of a non-bony conduit, running posteriorly along the medial face of the alveolar part of the maxilla. Other specimens, especially MMMP Nos. 281-S and 785-S (both *A. scagliai*), strongly suggest but do not quite conclusively demonstrate that this conduit left the orbital cavity through a foramen approximately dorsal to the posterior end of the palate, hence considerably posterior to the anterior part of the orbital space and to the usual position in marsupials or most other Theria. This peculiarity is consonant with the fact, to be considered below, that in argyrolagids the anterior part of the orbital space did not contain the eyeball and with the suggestion that it may have contained a slip of the masseter musculature.

The facial surface of the maxilla anterior to the infraorbital foramen is gently hollowed. The anterior root of the zygoma, formed by the maxilla, is lateral to M^{1-2} . It has a small but distinct ventral process. The maxillo-jugal suture cannot be surely identified, perhaps because of cracks in this area or perhaps because it is in fact closed, as often occurs in marsupials even

while many other sutures are still open. I also fail to detect the lacrimal or its foramen. It is possible, but only just possible, that it is at the anterior part of the dorsal rim of the orbit, as it is in *Dipodomys* and some other rodents but not in any marsupial known to me, other than these argyrolagids.

The posterior ends of the nasals are approximately above M^2 or M^3 . They are slightly expanded and have simply rounded sutures against frontals.

The orbit is among the most peculiar features of these altogether peculiar creatures. It is extremely large, and its orifice is directed mainly laterally but also somewhat dorsally and posteriorly. Anterior to the orifice, the cavity of the orbit extends forward for a distance almost two thirds that of the anteroposterior length of the orifice, but this extension is not visible laterally or dorsally. Dorsally it is roofed by a plate formed mainly by the frontal and maxilla but possibly including the lacrimal. Laterally it is covered by a plate probably composed mostly by the maxilla but probably also including the anterior end of the jugal and possibly the lacrimal. The surfaces here spoken of as plates have no evident separation and are essentially a single, curving surface, although the most dorsal part is essentially horizontal and the most ventral part essentially vertical, facing not simply laterally, but also anteriorly and slightly ventrally. In MMMP No. 785-S there are openings in each side of the dorsal surface of this plate, but these are probably artifacts and cannot be confirmed on the other specimens, none quite perfect in this region. The bottom of the anterior part of the orbital space, between the posterior part of the maxilla and the anterior end of the zygoma, is open.

Posterior to the anterior orbital roof, its edge continues as a sharp rim on the dorsal and posterior borders of the orbit. A similar rim continues from the anterior border of the orbital orifice along the dorsal part of the zygoma and then curves around the lateral and posterior sides of the dorsal

surface of the glenoid (or articular) process. At the posteroventral part of the orbit there is, in the two specimens of *A. scagliai* that have this region, a slight gap or lowering of the rim, and in the specimen of *M. reigi* with this region the rim is here definitely interrupted for a short space. With the stated exception, the rim of the orbit cuts off the whole space enclosed in the zygomatic arch from dorsal or lateral parts of the parietals and squamosals, which have smooth surfaces without sagittal, temporal, nuchal, or other crests.

This strange orbital and circumorbital anatomy raises serious questions as to masticatory muscles and functions. As close a structural analogue as I can find is again in *Dipodomys*, in which the orbit also extends anteriorly in a pocket covered by bone dorsally and dorsolaterally, somewhat as in the argyrolagids but less extensive. In *Dipodomys* the temporal musculature is greatly reduced. This must also have been true of the argyrolagids, which evidently had a miniscule single slip of temporal muscle originating on the squamosal above the meatus or possibly as far posteriorly as the mastoid. This correlates with the fact that the coronoid process of the mandible was certainly short (anteroposteriorly) in argyrolagids, as in *Dipodomys*, and probably also low, also as in *Dipodomys*. In *Dipodomys*, however, the weakness of the temporal muscle is balanced by a powerful masseteric complex, and the covering of the dorsoanterior part of the orbit is correlated with the origin of a large masseter major anterior to it. (For the osteology and myology of *Dipodomys* see especially Howell, 1932.) Such a muscle cannot have occurred in the argyrolagids. They doubtless had a masseter originating on the zygomatic arch and its anteroventral process, and perhaps another slip from the lateral face of the rostrum. It is logically probable that part of the masseteric muscular complex arose actually within the orbit in its anterodorsal pocket. This seems the

more likely as the origin of the masseter profundus of *Dipodomys* and some other rodents is, if not exactly the same, at least similar. The possible analogue of the masseter profundus in argyrolagids had not invaded the infraorbital canal as in the so-called hystricomorph rodents.

Much of the bizarre appearance of the argyrolagid skull is due to the unique structure and placing of the orbit. The anterior part of the orbital space, which is covered dorsally and laterally and cannot have contained a functional eye, is in the position of the orbit in "normal" mammals, or indeed "normal" vertebrates in general. The posterior part of the orbital space, which clearly contained the eye,¹⁵ is in the position of the temporal fossa. A functional temporal fossa, virtually universal in other mammals (and their ancestors and reptilian relatives), is here practically absent.

The broad frontals, not fused at the midline in the specimens including them, are smooth, slightly convex from side to side, somewhat domed posteriorly. The sutures against the parietals are transverse, slightly convex posteriorly. The frontals form at least the central part of the dorsal rim of the orbital aperture. Posterior and posteroventral to this the situation is not clear in the available materials, but it is probable that the parietals do not quite reach the apertural rim and that another element intervenes in the posterodorsal part of the rim. This could be the squamosal or the alisphenoid. The posteroventral part of the rim is formed by the squamosal, as are the glenoid process and posterior root of the zygoma. The glenoid surface is almost perfectly flat and is oval, with the

slightly longer axis anterolateral-posteromedial. From it the squamosal extends forward, as a tapering, jointed process forming the dorsal part of the zygoma, to the anteroventral part of the orbital rim. The jugal has a similar pointed process forming the ventral part of the arch, directed posteriorly and reaching the anterolateral part of the glenoid surface.

The parietals are smooth, broadly domed, and pass posteriorly into the supraoccipital without an intervening crest or ridge but with a decided change in curvature. The rounded occiput, directed for the most part posteroventrally, has a limited, almost equidimensional area for nuchal musculature above the relatively large foramen magnum and between the mastoids. The foramen magnum, transversely elliptical, is directed rather more ventrally than posteriorly, and its lower half is bordered by the narrow condyles, which almost, but not quite, meet ventrally. With the skull oriented on the alveolar or palatal plane, the condyles are directed almost straight ventrally. The head must have been carried approximately at right angles to the neck, which agrees with skeletal evidence that these animals were fully bipedal.

There is a large exposure of the mastoid between the auditory porus and the occiput. This is inflated, but on closer study rather less than might appear on first sight—the globular brain case gives an impression of inflation not really involving very large epitympanic sinuses such as occur in *Dipodomys*, for example. The whole region posterior to the orbitotemporal fossa is much shorter and narrower than in *Dipodomys* and is, in fact, quite like that of *Caenolestes*, despite some adaptive differences related to size, posture, and moderately increased inflation of the middle ear.

The porus acusticus is rather large and is directed posterolaterally and not at all ventrally, an unusual character. There is a tympanic ring, apposed but not fused to the bulla, not developed into a meatus, and closely similar to the tympanic of *Caeno-*

¹⁵ The hypothesis that this is, in fact, a temporal fossa and that a functional eye was reduced or lacking cannot be seriously entertained. In spite of its position this space has all the features related to a large eyeball and its muscles, and the relationship to the brain and cranial foramina is also appropriate. Moreover, these were certainly very active, saltatory animals that could not possibly have had reduced vision or none.

lestes except for the orientation of the aperture. On MMMP No. 785-S there is a small foramen above the porus. This may be homologous with the foramen identified as postglenoid in *Caenolestes* by Dederer (1909), if homology can be deduced from relationship to the ear rather than to the glenoid process. In *Caenolestes* the posterior root of the zygoma is above the porus, the glenoid surface is immediately lateral to the bulla, and the foramen in question is literally postglenoid. In *Argyrolagus* the root of the zygoma is anterior to the porus, and the glenoid is still farther anterior. The foramen is, indeed, posterior to the glenoid but so far away and so unrelated to it that "postglenoid" seems an inappropriate description or identification.

There is a closed alisphenoid bulla, considerably larger and more inflated than in *Caenolestes* or most other marsupials, ovoid with the axis directed posterolatero-anteromedially. This is relatively larger in the smaller *M. reigi* (MMMP No. 691-S) than in *A. scagliai* (MMMP No. 785-S).

The basicranium is partly preserved in the two specimens just mentioned, but most of the details are obscure in both. There appear to be carotid foramina and a transverse canal in the basisphenoid, much as in *Caenolestes* and many other marsupials. From the anteromedial point of the bulla on each side there is a short, small, longitudinal crest ending in a spicular process pointing anteriorly. Dorsolateral to these and immediately anterior to the bullae are two foramina, presumably the foramen rotundum and sphenorbital foramen. These are relatively much more posterior than in *Caenolestes*, or most other mammals for that matter. Their position is correlative with the extreme posterior position of the functional orbits and virtual absence of a temporal fossa. I cannot clearly make out other cranial foramina.

Skeleton. The following postcranial skeletal materials definitely referable to this family are available. Field data are here

given for specimens not included in specific hypodigms in the taxonomic section.

MMMP No. 785-S, associated with skull and jaws previously described, and part of the type of *Argyrolagus scagliai*. Atlas and eleven caudal vertebrae; sacrum and pelvis; fragment of scapula; parts of both humeri and of one radius and one ulna; both femora; both tibiae and fibulae (fused); five tarsals; metatarsals of both sides; three pedal phalanges.

MMMP No. 638-M. Humerus, lacking proximal end. Collected in May, 1956, by V. D. Martino in the coastal cliff between Arroyo Seco and Punta San Andrés. Probably Barranca de los Lobos Formation.

MMMP No. 693-M. Nearly complete humerus and distal end of another, perhaps same individual. In the same vial is another fragment of a humerus, not the same individual and probably not this family. From the upper level of the San Andrés Formation, 500 meters south of Punta San Andrés.

MMMP No. 795-S. Nearly complete humerus. Collected by O. Reig, 8 April 1952, south of the Arroyo Lobería. Bed II of the Vorohué Formation.

MMMP No. 395-M. A large lot of bones, mostly minor fragments. Parts of jaws in this lot are referable to *M. reigi*, and the lot has been listed in that hypodigm. The other fragments represent several individuals (at least three and probably more), some perhaps not of this family. The most useful specimens are three complete humeri, three nearly complete femora, and a calcaneum, representing probably two individuals of the same species.

MMMP No. 691-S. In addition to the skull of *M. reigi*, listed in the hypodigm and described above, this number includes a broken tibio-fibula labeled "Asociado al cráneo [de] *Microtragulus*." "Asociado" means that it was found with the skull but not necessarily that it belongs to the same individual. It is rather improbable that the skull and tibio-fibula, and nothing else, of one individual would be buried together.

However, it is highly probable that the tibio-fibula is of the same species as the skull, *M. reigi*.

MACN No. 4743. This number has been written, evidently at a later date, on Ameghino's label "*Microtragulus argentinus*" which accompanies the metatarsals that were his essential type for that species. The metatarsals are now in a separate small vial placed in a larger vial that bears the number 12925. In the larger vial are three articulated tarsals, which are probably the basis for Ameghino's reference to cuboid, scaphoid, and cuneiforms in his original description of *M. argentinus* (see taxonomic section, above). There are also fragments of five vertebrae, probably proximal caudals, not mentioned by Ameghino, and several nondescript scraps. It is not clear why these materials in the vial numbered 12925 are separated from the metatarsals, which must belong with the label numbered 4743, but the tarsals, at least, must be part of Ameghino's type or hypodigm of *M. argentinus*.

The skeleton will be described in this sequence: vertebrae, anterior girdle and limb, posterior girdle and limb. MMMP No. 785-S includes the atlas, sacrum, and eleven caudal vertebrae associated with the skull and jaws, type of *A. scagliai*. The atlas is in general stouter than in *Caenolestes* (for which, throughout this section, see Osgood, 1921), as befits a larger and, in all probability, more active animal. The arch is simple, but its mediodorsal part is expanded anteroposteriorly so that in dorsal aspect it appears not as a simple transverse band but as a strongly elongated ellipse or lozenge with rounded corners. The neural canal is not a simple ellipse but has the form of two widely connected ellipses, a larger above and a smaller below. This is suggested but is less pronounced in *Caenolestes*. The short transverse process has a relatively large vertebrarterial canal. Breaks on both sides have laid this open, but it was almost certainly a closed canal or, being short, a foramen in life. This is

not present in specimens of caenolestids known to me. Osgood (op. cit.) shows a "nutrient foramen" in this position, but that is so small that it probably could not contain a vertebral artery and is unlikely to be a homologue of the large opening in *Argyrolagus*. The neural canal is closed below by a relatively slender transverse bar with a short ventral process, much as in *Caenolestes*. The condylar articular surfaces are more complex in form than might be anticipated from the condyles themselves, as shown better in the illustration than by words. Above each there is a groove on the cranial side of the neural arch. The articular facets for the axis are fairly simple, widely separated ovals, about as in *Caenolestes*. A possible facet for the odontoid process is vague.

The sacrum consists of two ankylosed vertebrae, as usual in marsupials. Both the broad transverse process of the first sacral and the slender process of the second articulate fully with the ilium. There is a large vacuity between the processes of the two vertebrae. The prezygapophyses of the first sacral and postzygapophyses of the second are well developed, but those between the two are completely fused and form merely a vague prominence. A low medial crest represents poorly developed fused neural spines. The centra are compressed dorsoventrally. The neural canal continues through the sacrum, but is here quite small.

With this same specimen are four anterior caudal vertebrae, which articulate well enough with the sacrum and then with each other and so are probably the first four caudals. The prezygapophyses, present on all of them, are slender processes directed anterolaterally. They become progressively shorter on successive vertebrae. Shorter and narrower postzygapophyses are present on the first and second vertebrae and possibly on the third (here somewhat broken) but are absent on the fourth. All these four vertebrae have well-developed transverse processes, broken on

the first two caudals but probably also progressively shorter (transversely). The stout centra are dorsoventrally compressed. The presumed first caudal has a complete and relatively large neural canal, and this continues through the second, although narrowing rapidly. There are traces of it under the short neural arches of the third and fourth vertebrae preserved, but it is here so small as to be doubtfully functional. The first vertebra has a distinct, although broken, neural spine, but the next three have only a slight longitudinal ridge in this position. These four vertebrae considerably resemble what Osgood numbers as the second to fifth caudals in *Caenolestes* but are somewhat shorter, have more elongated prezygapophyses, and have traces, at least, of the neural spine. What Osgood calls the first caudal is fully fused, both medially and at the ends of the transverse processes, with the preceding unquestionably sacral vertebra. Its transverse processes do not quite touch the ilia in dried, noncartilage skeletons, but it might well be considered sacral or, at least, pseudosacral rather than flatly caudal. In any case, no third vertebra was fused with the sacrum in *Argyrolagus*.

The five poorly preserved vertebrae mentioned above as probably associated with the type of *Microtragulus argentinus* also are probably anterior caudals. If so, that species, at least, had not less than five caudals generally similar to the four just described for *Argyrolagus scagliai*. They are smaller than those of *A. scagliai* in about the same proportion that the metatarsals are smaller. They also have broader, more flattened neural arches and less protruding zygapophyses.

With MMMP No. 785-S, *A. scagliai*, are seven more posterior caudals, possibly but not certainly successive among themselves and to the four described above; thus they are perhaps caudals five to eleven, and, are certainly not more anterior than those. As in *Caenolestes*, they are abruptly unlike the more anterior caudals. The stout centra

are much more elongated, there are no neural canal, transverse processes, or zygapophyses. On the first one or perhaps two there are vestiges, only, of a neural arch. All the vertebrae have paired, nubbinlike dorsal and ventral processes at the anterior end and paired, somewhat alar, lateral expansions at the posterior end. The apparently most posterior of these vertebrae is almost as long as any of the others and only moderately more slender. As would be expected in a bipedal, saltatory animal, *Argyrolagus* clearly had a long, heavy tail, much as in kangaroo rats and jerboas. However, *Caenolestes* and some other quadrupeds also have long, stout tails.

The scapula is known only by a scrap of its distal end, part of the same specimen, type of *A. scagliai*. There is nothing particularly distinctive about this. The spine in its distal part seems relatively anterior, but as the prespinous part of the blade probably expanded above this, the spine may have been about medial over-all, as in *Caenolestes*. The acromion is broken away, and its shape or extent cannot be judged. The distal part of the posterior part of the blade has a somewhat thickened rim. The articular fossa is an antero-posteriorly elongate oval. The base of the coracoid process is rather stout, but the process itself is broken away.

The same specimen includes most of the left humerus, lacking the proximal end, and the distal half of the right humerus. There is a well-developed deltoid ridge, somewhat shorter (proximodistally) but somewhat more expanded than in *Caenolestes*. There is a large entepicondylar foramen, as in *Caenolestes*, but differing in that there is a projecting crest anterior to its medial opening, so that opening is not visible in anterior view, both openings, however, are visible in a slightly posteromedial view. The supinator ridge differs markedly from that of *Caenolestes*, being much more prominent and more elongated proximodistally. On the right humerus of this specimen, where it seems to be un-

broken, its lateral edge does not flair beyond the ectocondyle but it is almost straight proximodistal. The distal articulations of these specimens do not differ markedly from those of *Caenolestes*. In both humeri there is a supratrochlear aperture that seems to be a natural foramen.

MMMP No. 638-M, a humerus also lacking the proximal end, is similar to those just described, even to having a probable supratrochlear foramen. All the other humeri listed above also have apertures in this position, although that of MMMP No. 396-M is very small. In no case can artifacts be absolutely ruled out, but this repetition makes it extremely probable that a natural foramen here characterizes the group.

In the lot catalogued as MMMP No. 395-M there are three nearly complete humeri. Two, although not exactly alike, are possibly from one individual. The other is obviously from a different individual and is somewhat larger. In all the supinator ridge flairs strongly externally above and lateral to the ectepicondyle, thus differing from MMMP No. 785-S, which certainly is *A. scagliai*, and 638-M, which probably is. The width across the distal articulation (trochlea plus capitulum) is relatively and absolutely less in 395-M. The argyrolagid teeth in this lot are of *Microtragulus reigi*, and the femora, significantly smaller than those known for *A. scagliai* (see below), almost certainly are also. It therefore seems probable that these humeri belong to *M. reigi*. This is supported to some, but not a conclusive, degree by the facts that only *M. reigi* has been positively identified from teeth in the formation from which they come (Barranca de los Lobos), and that if these humeri do not belong to *M. reigi*, none of those known do. These are somewhat smaller than humeri referred to *A. scagliai*, but the teeth, skull, and femora referred to *M. reigi* are still smaller than those of *A. scagliai*. There is thus a reasonable probability that

M. reigi had relatively larger front legs than did *A. scagliai*. These humeri preserve the proximal ends, which are not particularly distinctive and closely resemble those of *Caenolestes*, including the fact that the so-called lesser tuberosity is higher and more prominent than the so-called greater tuberosity.

The other known humeri, MMMP Nos. 396-M and 795-S, do not add to morphological knowledge and are of uncertain affinities, being to some extent intermediate between those referred to *A. scagliai* and *M. reigi*.

The right ulna is completely preserved in MMMP No. 785-S. It is generally quite similar to that of *Caenolestes* but somewhat stouter, relatively deeper anteroposteriorly. The olecranon is about equally long. The distal end is stout and has a distinct but short styloid process. The proximal end of the right radius of the same specimen is preserved. It was entirely free of the ulna, as was the distal end, as shown by the ulna. Its head is circular and it has a definite, strong tuberosity. No tuberosity is seen on the ulna, but it is slightly damaged in this region.

No bones of the manus are known.

Except for the blade of the left ilium, the pelvis is almost completely preserved in MMMP No. 785-S. It is radically unlike the pelvis of *Caenolestes*. Many, although not all, of the differences are resemblances to saltatorial rodents and hence may be considered locomotory adaptations adding to the many other convergent characters among argyrolagids and, especially, kangaroo mice and jerboas.

Howell (1932) has pointed out some supposed trends in transition from quadrupedal to extreme bipedal saltatory locomotion in rodents. Although Howell's conclusions seem to be invalid or, at best, unsubstantiated,¹⁶ the homologous figures

¹⁶ Measurements on Howell's fig. 15 differ radically from the figures given on p. 519, and my figures for *Dipodomys* also differ greatly from his. He has either taken the measurements in

in Table 3, based on my measurements, are of interest (p. 66). The length of the ischium relative to the ilium is about the same in *Argyrolagus* and *Caenolestes* and is slightly, perhaps not significantly, greater in a specimen of *Dipodomys*. This proportion has no evident relationship to bipedality. On the other hand, the postsacral part of the ilium is much longer, which is also to say that the presacral extension of the iliac blade is relatively much shorter, in *Caenolestes* than in *Dipodomys*. In *Argyrolagus* this difference is still greater, the presacral part being actually longer than the postsacral. This does seem to be a bipedal-saltatory specialization.¹⁷

The great anterior extension of the ilium is accompanied by the flaring of the upper lateral, strongly concave, gluteal surface. The lower lateral, presumably iliac surface, also concave, is smaller. The ridge between them is prominent, as is the tubercle at its posterior end, near the acetabulum. The strong tuberosity of the ischium is the most posterior point of the pelvis, the posterior border ventral to this down to the symphysis being almost vertical but inclined slightly forward. In striking contrast with *Caenolestes*, the symphysis is long, its anterior end below the acetabulum.

The ascending part of the pubis thus is nearly vertical. It almost certainly was not in contact with a marsupial bone throughout the length of its anteroventral edge, as it is in *Caenolestes*, but whether a marsupial bone with less extensive contact was present cannot be determined. The acetabulum is deep, with heavy, high dorsal and anterior rim, but is not otherwise characteristic. There is a low ileopectineal

tubercle. The component bones of the pelvis are all fully fused, at the symphysis as well as elsewhere. The pelvic aperture is rather shallow and wider than deep. This and the fused symphysis accord with marsupial reproduction, with extremely small offspring at parturition. (In *Dipodomys* and many other small placentals the aperture is deeper than wide; the symphysis is unfused and the two sides of the pelvis here separate when parturition of the relatively large young occurs.)

Both femora are present, only slightly damaged, in the type of *A. scagliai*. The femur is closely similar to that of *Caenolestes*; the most striking distinction is not structural but is that the femur of *Caenolestes* is shorter than the humerus, whereas in *Argyrolagus* it is more than twice as long as the humerus. The head is approximately spherical and almost sessile, with a short, barely constricted neck. The greater trochanter extends proximally distinctly above the head of the right femur but not quite up to the level of the head on the left femur. Both have been affected by crushing, and the original condition was probably intermediate. The digital fossa is long and slitlike, almost exactly as in *Caenolestes*. The intertrochanteric ridge is present but forms a somewhat rugose mass rather than a crest, and its extremity is distinctly separate from the lesser trochanter, which is flaring and proximal. A smaller third trochanter is distal to the greater trochanter, opposite the lesser trochanter but with its apex slightly more distal. The long shaft, almost circular in section, has a graceful sigmoid curve, slightly concave anteriorly in the proximal part and convex in the medial and distal parts. The distal end has a broad, shallow patellar groove, strongly suggesting but not proving the existence of a bony patella.

The three femora under MMMP No. 395-M are not quite so well preserved. They are closely similar to those just described but are decidedly smaller and somewhat more slender. The neck may be

some different way or has entered them incorrectly at some point in his research. Moreover, further on p. 519 his figures show an increase in distance from acetabulum to sacral articulation with increasing bipedalism, but in the next sentence he says that the distance has been shortened.

¹⁷ As Howell (1932) concluded, although his numerical values seem to show the opposite. Howell did not find a satisfactory functional explanation.

more constricted, the intertrochanteric ridge less definite, and all the proximal features less strongly developed, but these may be effects of faulty preservation. These bones almost certainly belong to *M. reigi*. As previously noted, they are somewhat smaller relative to the humeri believed to be of that species (or the humeri are somewhat larger relative to them) than in *A. scagliai*.

The tibia and fibula, known in MMMP No. 785-S, are fused proximally just at the point of contact and with a visible line of separation. Distally, from about the middle of the shafts onward, they are completely fused, with no visible line of separation. A greater or less degree of fusion occurs in kangaroo rats, jerboas, hares, and some other leaping placental but not in caenolestids. The proportions and general characters are, however, otherwise rather *Caenolestes*-like. The proximal half, approximately, of the tibia is triangular in section, with a greatly produced cnemial crest reaching its greatest eminence about one-sixth of the way down the shaft and thereafter gradually fading out. The anteromedial face is gently convex, the anterolateral hollowed out and more strongly concave. The much shorter posterior face, somewhat bowed forward, is gently convex from side to side, with a slight medial longitudinal ridge in its upper part. The whole tibia in this proximal portion is bowed anteromedially away from the fibula, which is almost straight. The distal part of the shaft of fused tibia and fibula is polyhedral in section, with six angulations of varying prominence. The tibial part of the distal end has the usual articulation for the astragalus and a well-developed internal malleolus. The fibular part, projecting beyond the astragalar articulation, has a well-developed facet that articulates with the calcaneum.

MMMP No. 691-S includes a tibiofibula lacking the distal end and imperfect elsewhere, referred with little doubt to *M. reigi*. The preserved parts compare closely

with the latter, but the cnemial crest is even more produced proximally, although it falls away more abruptly and at a less distal point.

An astragalus, both calcanea, a cuboid, an ectocuneiform, and a possible navicular of *A. scagliai* are preserved with MMMP No. 785-S. The body of the astragalus is larger than the head and the broad, very shallow trochlea occupies almost its entire width on the dorsal (or anterior) side. The head is not quite as wide as the body and is very short and sessile, without a distinct neck. On the ventral (or posterior) surface the trochlea ends in a sharp flange overhanging the sustentacular and part of the ectal facets. Those two facets are of nearly equal size, the ectal concave and the sustentacular more nearly plane, almost in contact with each other but at slightly different levels. There is no astragalar foramen. The most decided difference from *Caenolestes* is the less distinct, less projecting head.

The tuber of the calcaneum (or os calcis), unlike that of *Caenolestes*, is stout, decidedly longer than the body of the bone, and expanded posteriorly. The ectal facet, central on the body, is moderately convex, and the sustentacular facet, not clearly separated from the ectal and at a slightly lower (or more posterior) level, is more distinctly convex. Internal and slightly distal to these facets is a third of about equal size, transversely semicylindrical. This articulates with the fibular side of the distal end of the tibiofibula and is either absent or much less definite in *Caenolestes*. A small tubercle disto-external to this is probably homologous with what Osgood (1921, p. 96 and pl. XVI) calls in his text a facet for the tarsometatarsal ligament and in his figure a facet for a ligament to the astragalus of *Caenolestes*. On the dorsal or anterior surface the bone projects beyond the ectal, sustentacular, and fibular facets at a lower, or more posterior, level. The distal, cuboid facet is distinctly double. The external part extends farther distally

and is more convex. Between the two is a short, sharp step, along which contact with the cuboid continues. There is a hint of this rather odd condition in *Caenolestes*, but it is not so distinct.

In correlation with the peculiar cuboid facet of the calcaneum, the proximal surface of the cuboid has two facets and a step between them, the external facet more distal. The distal surface of the cuboid articulates strongly with metatarsal IV and lightly with the process on it interpreted below as the fused proximal end of metatarsal V. The cuboid probably associated with the type of *Microtragulus argentinus* is closely similar but smaller, as are all known parts of that species.

There is doubt about the navicular. In the partial tarsus probably of *M. argentinus* there is a bone articulated in this position. It articulates with a single bone, presumed to be the ectocuneiform, distally on the anterior or dorsal surface. This distal part projects more posteriorly than the presumed ectocuneiform, and if there were meso- and entocuneiforms they must have been very small and have lain here rather than in the more usual position medial to the ectocuneiform. Above this posterior or plantar part of the mooted navicular, a long and stout styloid process projects proximally. It is possible, but improbable, that this bone has not been articulated correctly and that it is not in fact a navicular or is a wrongly oriented navicular. With MMMP No. 785-S there is a bone of somewhat similar but far from identical shape, which I cannot articulate satisfactorily with other preserved parts. It may or may not be a navicular. In this individual the probable ectocuneiform is articulated with the left metatarsals and there is indeed a small posterior space that could have contained one or two more cuneiforms.

As previously noted, the essential type of *M. argentinus* consists of metatarsals III and IV, and these, both left and right, are also present in the type of *A. scagliai*. These bones in the two species are practi-

cally identical in character except that those of *A. scagliai* are decidedly longer and slightly stouter. Contrary to Ameghino's belief, and mine on first sight, metatarsals III and IV of *M. argentinus* are not fused and therefore do not form a true cannon bone. They are very closely appressed, with flat, slightly irregular contacting surfaces, and they adhered to each other through fossilization, as did several of the nevertheless separate tarsals. Separate motion of the two metatarsals or motion of one relative to the other must have been quite limited or nil. The metatarsals of MMMP No. 785-S, *Argyrolagus scagliai*, have also adhered to each other, and I have not ventured to try separating them. However, it seems highly probable that, as in *M. argentinus*, they are appressed but not fused. These bones also have the peculiarity that the two, together, are slightly skewed. If the proximal parts of the two bones, in normal contact, are placed on a flat surface, a line across the distal ends is not parallel to that surface, but the end of metatarsal IV is above it, or is relatively more anterior or dorsal than the end of III.

Those distal ends are slightly divergent and are of the same length, that is, are equally distal. Their phalangeal articulations are globular anteriorly, transversely cylindrical posteriorly, there each with a median keel. Proximally the metatarsal believed to be IV projects slightly farther than the other. It articulates with the bone interpreted above as the cuboid. In this individual a tarsal, interpreted as the ectocuneiform, is preserved in articulation with the left metatarsals. Its distal articulation is with the more medial metatarsal, believed to be III, only. On this specimen there is a separate slip of bone extending down onto the posteromedial surface of metatarsal III but there quickly wedging out. Proximally it is stouter but extends almost as far as the cuneiform. The other metatarsal III of this individual and the type of *M. argentinus* have articular facets

for this bone. It could be a mesocuneiform, but it seems more probable that it is a much reduced metatarsal. In either case, there was no digit on this side of the bone identified as metatarsal III. On the side of the proximal end of metatarsal IV there is a short styloid process, distal to which there is a posteromedial swelling of the bone quickly dying out in the distal direction. There are slight concavities between this and the body of metatarsal IV but no distinct line of fusion. Ameghino (1904) interpreted this (in *M. argentinus*) as the fully fused, functionless, proximal end of another metatarsal. This is probable, although not certain. In any event, no facet for apposition of another separate metatarsal is visible here. The conclusion is almost forced, although perhaps not absolutely certain, that these animals had only two toes on the pes, without even vestiges of others beyond the proximal ends of the metatarsals.

The homologies of the two fully developed metatarsals are of importance both functionally and phylogenetically. Believing *Microtragulus argentinus* to be a ruminant artiodactyl, Ameghino (1904) naturally considered the supposed cannon bone to be formed by metatarsals III and IV, and as far as I know all later students have accepted that without further discussion. However, if *Argyrolagus* were a diprotodont or phalangeroid, as L. Kraglievich believed and Rusconi agrees, that homology would be virtually impossible. In all phalangeroids, metatarsals II and III are reduced and the corresponding digits are syndactylous and always somewhat, usually much, shorter than IV, often also shorter than V. As further treated in discussion of relationships, such feet are basic for diprotodonts and probably antedated the origin of that group as such. If *Argyrolagus* had that ancestry, its supposed cannon bone (the two large, appressed metatarsals) would practically have to be IV and V. However, in that case these two bones together would articulate largely

or wholly with the cuboid proximally. In fact, each of the two articulates wholly with a quite separate tarsal. There can be little doubt that these are the cuboid and ectocuneiform, that the tarsals are, indeed, III and IV, and that Ameghino was right (for the wrong reason). Such a foot could readily evolve from a more generalized one as in *Caenolestes*,¹⁸ but not from a perameloid or phalangeroid foot.

MMMP No. 785-S included two proximal and one distal phalanges. The proximal phalanx is arched dorsally (or anteriorly). The concave proximal articulation is at an angle of about 45° with the long axis of the bone, suggesting that the toe was normally carried at an angle of about 135° with the metatarsal. This articulation is notched proximoventrally, corresponding with the metatarsal keel. On the plantar side there are convex nubbins on each side of the notch. The distal articulation is simply convex in a longitudinal direction and straight in transverse section. It is mostly on the plantar side of the bone. The distal phalanx is a sharp, only slightly recurved claw, strongly compressed from side to side. The articulation is a semilunar notch directed proximoplantarly. Anterior to it on the plantar side is an elongated projecting process, swollen at proximal and distal ends. This terminal phalanx seems small and weak in proportion to the proximal phalanx and other limb bones, but the probability is great that it does belong to the same individual.

AFFINITIES

Former views. Ameghino (1904) based *Microtragulus argentinus* on two supposedly fused metatarsals, or a "cannon bone," mentioning also other metatarsals, cuboid, scaphoid (=navicular), and cuneiforms, without description further than

¹⁸ In his generally excellent monograph on *Caenolestes* Osgood (1921, pp. 96-97 and plate XVI) has misidentified the cuneiforms, and his statement of their relationships to the metatarsals is impossible.

saying (in Spanish) that they were "constructed, like the other bones, on the same type as the Tragulidae." Apart from reference to the Tragulidae, no further discussion of relationships was given pending "a special notice accompanied by figures" (in Spanish). That notice was never published, but in his final polemic stratigraphic volume (Ameghino, 1906, p. 344) a figure (fig. 177) of the metatarsals, only, was given along with the following remark:

"What I never suspected was that the selenodont artiodactyls might also be of South American origin. That origin is indicated by the recent discovery at Monte Hermoso of part of the skeleton of a tiny artiodactyl that has been given the name of *Microtragulus argentinus*."¹⁹

This seems clearly to indicate that Ameghino then considered *Microtragulus* as ancestral or prototypal for selenodont artiodactyls. That was, however, anomalous even from Ameghino's own point of view. He considered *Microtragulus* as late Miocene in age, and selenodont artiodactyls that he considered older, Oligocene at least, were already well known from North America and Europe. He later (Ameghino, 1912) still considered *Microtragulus* as "the smallest and most primitive known selenodont artiodactyl" (original in French), yet not as ancestral to all other selenodonts, and as African, not South American nor yet North American, in origin. The geographic aspect of that is considered elsewhere in this study. The point here is that Ameghino continued to consider *Microtragulus* as a primitive selenodont artiodactyl.

As far as I have been able to discover, that opinion was never accepted by anyone else. L. Kraglievich said in passing that *Microtragulus* might be a rodent or a

diprotodont marsupial (1932), and he later (1934) listed it as a rodent. Castellanos (1934) said, also in passing, that it is not an artiodactyl but a rodent. Those opinions seem to be the only ones expressed after Ameghino and before the close relationship of *Microtragulus* and *Argyrolagus* was recognized.

The type lower jaw of *Argyrolagus palmeri* was discovered in the same beds, those of Monte Hermoso, at approximately the same time, early 1904, and by the same collector as the type of *Microtragulus argentinus*. The earliest opinion as to the affinities of *Argyrolagus*, although not published until much later, was expressed by the collector, Carlos Ameghino, in a letter to his brother Florentino dated from Monte Hermoso on 11 May 1904:

"Of rare genera, besides the ursid already mentioned, there finally has come to light a plagiaulacid, which I had a sort of yen to discover. It is a very small lower jaw, as small as *Epanorthus minutus*, but very peculiar. Its aspect is surprising, the molars apparently with open roots, somewhat like those of *Pithanotomys*, and it seems quite likely to me that this is that extremely rare genus known as *Tribodon clemens*. The dental formula comprises four true molars and a small styliform premolar, and the incisor is as in the paucituberculates of Santa Cruz. I believe it is a descendant of *Promysops* of the *Notostyllops* beds."²⁰

²⁰ "De géneros raros, además del Ursídeo ya mencionado, ha aparecido, al fin, un Plagiaulacéido, que tenía como antojo de encontrar. Es una mandíbula inferior muy pequeña, tanto como *Epanorthus minutus*, pero muy singular. Es de un aspecto sorprendente, con los molares al parecer de base abierta, algo parecidos a (los de) [probably an insertion by the editor] *Pytanotomys* [sic!] y me parece muy probable que se trate de aquel género rarísimo conocido por *Tribodon clemens*. La fórmula dentaria se compone de 4 verdaderos molares y de un pequeño premolar anterior estiliforme y el incisivo es como en los Paucituberculados de Santa Cruz. Yo creo que es un descendiente de los *Promysop* [sic!] del *Notostilopense*."

¹⁹ "Ce que je n'avais jamais soupçonné c'est que les artiodactyles sélénodontes pouvaient être aussi d'origine sud-américaine. Cette origine est indiqué par la découverte faite récemment à Monte-Hermoso, d'une partie de squelette d'un tout petit Artiodactyle qui a reçu le nom de *Microtragulus argentinus*. . . ."

The plagiaulacids, strictly speaking, are late Jurassic and early Cretaceous multituberculates. In the Ameghinian system, however, the term referred loosely to an assemblage including also Polydolopidae and Caenolestidae and believed to extend, in part ancestrally, to the Australian diprotodont marsupials and the placental rodents and lagomorphs. (Ameghino did not consider marsupials and placentals as distinct taxonomic groups.) *Epanorthus* is a caenolestid, but Carlos Ameghino refers to it only for comparison of size, not as a matter of affinity. *Pithanotomys* and *Tribodon* are both (true placental) rodents from Monte Hermoso. Don Carlos not only indicates this as a true relationship but also considers it likely that this specimen belongs to a species of *Tribodon*. *Promysops* (= *Eudolops*) is a polydolopid marsupial. The Ameghinos considered this genus ancestral to placental rodents and lagomorphs. Don Carlos's opinion that this specimen is a descendant of *Promysops* thus does not contradict his belief that it might belong to *Tribodon*, a genus of rodents.

In referring to this letter, then unpublished but evidently read by him, Rusconi (1933) said that Don Carlos had considered this mandible as "somewhat related to the marsupials of Patagonia." He later (Rusconi, 1967, p. 283) said that Carlos Ameghino, in the letter here cited, had identified *Argyrolagus* as a marsupial of the group of the Paucituberculata (= Caenolestoidea). He then contrasted Don Carlos's field identification, believed to be at least approximately correct, with the incorrect cabinet identification by "Dr. Florentino." In fact, Don Carlos did not identify *Argyrolagus* as a marsupial or a paucituberculata. He clearly stated his belief that it was a rodent and even indicated possible pertinence to a previously named genus of rodents. The only suggested connection with marsupials depended on the Ameghinos' belief (now of course known to be unfounded) that all rodents (and lagoon-

morphs) were derived from forms that we now classify as marsupials.

When he first published on this specimen, Florentino Ameghino (1904) agreed with Don Carlos in considering *Argyrolagus*, then named, a rodent *sensu lato*, but rather as a duplicidentate, that is, a lagomorph, than a simplicidentate.

"The representatives of this new family . . . from the original stock for the Lagomorpha or duplicidentates and are the most primitive known rodents. The discovery of this family solves the hitherto mysterious origin of the duplicidentates, showing that they arose from the Promysopidae independently of the other rodents."²¹

As noted previously, *Promysops* is in fact a polydolopid and is synonymous with a genus, *Eudolops*, that Ameghino himself referred to the Polydolopidae. However, that does not matter much as regards Ameghino's views on *Argyrolagus*, since he believed that the "Promysopidae," and hence through them both lagomorphs and rodents, were earlier derived from the Polydolopidae. It does matter that Ameghino considered *Argyrolagus* implicitly as ancestral to and explicitly as more primitive than the lagomorphs, although he believed it to be late Miocene in age and knew of North American Oligocene lagomorphs. He later (Ameghino, 1906) made it clear that he considered the Agyrolagidae ancestral to the lagomorphs through (unknown) earlier members of the family and not through the late genus *Argyrolagus* itself. He then figured the type specimen of *Argyrolagus palmeri* (Ameghino, 1906, p. 368, fig. 221).

Like *Microtragulus*, *Argyrolagus* was long ignored by most other students of South American mammals, or of mammals

²¹ "Los representantes de esta nueva familia constituyen el tronco de origen de los Lagomorpha o duplicidentados y son los roedores más primitivos que se conocen. El descubrimiento de esta familia viene a resolver el origen de los duplicidentados que era hasta ahora un misterio, demostrando que se han separado de los *Promysopidae* independientemente de los demás roedores."

in general. For example, it figured neither in Scott (1913) nor Schlosser (1923). However, L. Kraglievich (1931) later refigured and redescribed Ameghino's type and added another species, *A. catamarcensis* from the Araucanian beds. He noted correctly that the structure is quite different from any lagomorphs, but resembles diprotodont marsupials, by which he meant the Australian group I (e.g., Simpson, 1945) call Phalangerioidea, excluding the Caenolestioidea (Paucituberculata of Ameghino and Kraglievich). The only resemblances definitely stated were: the shapes of the inflected angle and masseteric flange, compared with those of *Trichosurus*; the presence of a masseteric foramen, correctly stated to be present in some but not all phalangerids; and the number and form of the incisors and molars, said to show affinities with phalangerids but not more explicitly compared. He also said that there are slight resemblances (one must so understand "ligeras afinidades") with the Paucituberculata (Caenolestioidea), but that *Argyrolagus* differs much more from them than from the phalangerids. However, no difference from the caenolestoids was specified. In fact, the angle and masseteric flange are quite like those of recent caenolestids, and these also have a masseteric foramen more like that of *Argyrolagus* than is that of *Trichosurus*. The lower dental formula of *Argyrolagus* is in fact like that of *Trichosurus* and other relatively primitive phalangerids: $\frac{2.0.1.4}{3.1.2.4}$. However, the upper formula (unknown to Kraglievich) is not; $\frac{4.1.3.4}{3.1.3.4}$ is primitive for phalangerids, but the formula is $\frac{2.0.1.4}{3.1.3.4}$ in *Argyrolagus*. The whole *Argyrolagus* formula could just as well be derived from the primitive caenolestid formula, $\frac{4.1.3.4}{3.1.3.4}$, and the form of the teeth of *Argyrolagus*, especially the incisors, differs greatly and about equally from both recent phalangeroids and recent caenolestoids, none of which have two enlarged, rodentlike incisors in the lower (and still less in the upper) jaw.

Thus Kraglievich did not in fact give any valid reason for referring *Argyrolagus* to the Phalangerioidea or for excluding it from Caenolestioidea. He further and correctly excluded "Promysopidae" (= Polydolopidae) and Polydolopidae from ancestry to this genus, but his statement that the ancestry therefore did not occur in Patagonia is a non-sequitur, and in any case absence from Patagonia would not argue against caenolestoid or for phalangeroid affinities. Kraglievich was, however, on safe grounds in recognizing the Argyrolagidae as a distinct family, whatever its affinities may be.

Shortly after publication of Kraglievich's paper, Rusconi (1933) described still another presumptive species, *A. parodii*, from the Chapadmalalan. He then adopted Kraglievich's views as to affinities, saying (in English) that "there is no probability of the existence of a link between [the Polydolopidae and Caenolestidae] and the *Argyrolagus* group," and deriving the "argyrolags" from "primordial phalangerids." He supposed the low position of the condyle of *Argyrolagus* to be archaic but the dentition to be highly specialized and supposed that "the ancestry of the argyrolags can be traced successfully in this manner." Neither of these characters is phalangeroid, and no evidence of such affinities was given except citation of Kraglievich. "The paucituberculated marsupials of Patagonia," that is, fossil caenolestoids, are said to "represent a group of mammals that evolved in a different way from *Argyrolagus*."

In the meantime, before Rusconi's paper was published, I (Simpson, 1932) pointed out the improbability and inadequate evidence of special affinity between *Argyrolagus* and Australian diprotodonts and hazarded a guess that it might be an aberrant tyothere. That guess was extremely wide of the mark, although my principal point of non-community of origin with the phalangeroids can still be sustained.

When Rusconi wrote his paper of 1933, he had not seen mine of the previous year. He later (1936) firmly rejected reference to the Typotheria and insisted on marsupial affinities. He was quite right on both counts. In that same paper Rusconi (1936, p. 181 or p. 11 of the separate) said, "My *a priori* impression is that the cannon bone of *Microtragulus argentinus* would seem to belong in the hind limb of *Argyrolagus*, an idea with which Don Carlos Ameghino, its discoverer, also agrees."²²

In discussion of affinities in that paper, Rusconi was primarily concerned with proof that *Argyrolagus* is not a typothere. He gave a list of thirteen non-typothere characters and said that five of these are typical of many marsupials: last molar bilobed, second lobe small; strong perpendicular masseteric crest below last molar; large masseteric fossa with a masseteric foramen; strong, inflected angular process; probable dental formula I.0.I.4. Not all of these non-typothere characters are diagnostically marsupial, but the case is made. In addition, Rusconi called attention to the canal behind the last molar and noted that it occurs in some paucituberculates (caenolestoids) in the Tertiary of Patagonia. (It also occurs in recent caenolestids.) No more evidence of phalangeoid affinities was given, and no definite statement of the place of the argyrolagids in the Marsupialia, although there is an implication that they are not considered caenolestoids.

In view of all that discussion and of his frequent distrust of Ameghino's work, it is peculiar to find Scott in 1937 (p. 240)

no longer ignoring *Argyrolagus* but assuming that Ameghino was right in calling it a lagomorph, indeed a rabbit.

Since Rusconi's paper of 1936, synonymy of *Argyrolagus* and *Microtragulus* and reference to the Marsupialia have been accepted by a few writers, but there has been no further first-hand published research and little mention of this group. For example the family is not mentioned in the almost exhaustive French *Traité*s of zoology and of paleontology. Following Rusconi's paper of 1936, I (Simpson, 1945) provisionally accepted reference of *Argyrolagus* to the Marsupialia. In 1955 Reig (1955, p. 61) formally indicated synonymy of *Argyrolagus* with the prior name *Microtragulus*, named the family Microtragulidae, and referred it to the Caenolestoidea. That was done on the basis of specimens, then unpublished, described in the present study (Reig, 1955, footnote on p. 60). Reig later (1958, p. 249) again indicated the generic synonymy and listed the Microtragulidae among the Marsupialia.

Romer (1966, p. 379) has listed the "Microtragulidae" with "*Microtragulus* [*Argyrolagus*]" in the Polyprotodonta, which he distinguished both from the Caenolestoidea and from the Diprotodonta. Affinities are not discussed, but the hierarchical and sequential arrangements imply separate origin from the Didelphidae.

Most recently Rusconi (1967, p. 284) has again noted that *Argyrolagus* and *Microtragulus* (which is consistently misprinted "*Microtagulus*" and in Spanish vernacular "*Microtagulo*") may be synonymous, but he is rather less positive than in his 1936 paper and he fails to note that in case of synonymy it is the name *Argyrolagus* that is invalidated. He continues to consider these animals as related to the Australian diprotodonts (misprinted "diprodontes" in the Spanish text) rather than to any other South American marsupials. He now definitely refers the Argyrolagidae to the otherwise Australian superfamily Phalangerioidea. (He erroneously also includes

²² "Mi impresión, *a priori*, es que el *os canon* de *Microtragulus argentinus* parecería corresponder al miembro posterior de *Argyrolagus*, ideas [sic, plural] a la cual se adhiere también Don Carlos Ameghino, su descubridor."

It is not clear to me in what way this idea is to be considered as *a priori*.

The agreement by Carlos Ameghino was presumably in personal communication. Don Carlos, long chronically ill, died in the year of the publication in question.

New Zealand in the distribution of the superfamily.) No new evidence for this view is given.

Present views. The argyrolagids are now fairly well known, thanks to the specimens described in this account, and there is a relatively good basis for determining their affinities. Nevertheless they are so peculiar that their status remains somewhat dubious even now.

These animals are unquestionably marsupials. No single one of their known characters would be typologically diagnostic (none is present in all marsupials and no placentals), but the following combination of characters is conclusive:

Four molariform teeth and less than four premolars.

Large palatal vacuities.

Alisphenoid bullae.

Probable transverse canal and entocarotid foramina in basisphenoid.

Angular process of mandible strongly inflected.

Masseteric foramen present.

Long, fused pubic symphysis and shallow pelvic outlet.

The presence or absence of a marsupial (epipubic) bone, highly characteristic of marsupials but not present in all of them, has not been determined. If present, its contact with the pelvis was slight and non-sutural, but that is common in (other) marsupials.

The present question, then, is not whether the argyrolagids are marsupials—they certainly are—but where they belong among the varied ranks of marsupials. Here the first point, obvious throughout the preceding descriptions and the illustrations, is that argyrolagids have many peculiarities that are rare, less developed, or completely absent in any other known marsupials. The most striking of these are:

Presence of two, somewhat rodentlike, rootless incisors in each side of each jaw, upper and lower.

Five continuously growing cheek teeth on each side, above and below.

Very long snout, projecting as a closed bony tube anterior to the upper incisors and palate; palate short.

Large anterior orbital space covered by bone dorsally and laterally.

Eyeball in extreme posterior position.

No distinct temporal fossa.

Globular cranium with some hypo- and hypertympanic inflation.

Metatarsals III and IV appressed, extremely elongated.

Only two functional toes in pes.

Other peculiarities represent functional specializations that occur in more or less similar form, evidently by convergence, in a number of different groups, both marsupial and placental. Most obvious of these are the characters associated with bipedal saltation, such as the small fore legs, enlargement and distal elongation of hind legs, and long, heavy tail.

These and other less striking but also peculiar characters show that the argyrolagids are an extremely aberrant, highly specialized group. Surely no one could question their reference to a distinct family, as proposed by Ameghino from the start and accepted without reservation in every subsequent reference to the group (as represented by *Argyrolagus*). The questions then are (a) at what hierarchic level, family or higher, the argyrolagids should be separated from other marsupials, and (b) with what other taxon, if any, below the level of subclass or infraclass Metatheria the argyrolagids may be naturally²³ associated.

²³ By "naturally" I of course mean evolutionarily or phylogenetically. Phenetic classification, sometimes wrongly called "numerical," if pursued without any evolutionary concepts, would almost certainly classify argyrolagids not as marsupials at all but as rodents rather closely related to Dipodidae, Heteromyidae, or both. I believe that this is a case in which the most extremely exclusive pheneticists will find the combination of phenetic evidence with evolutionary interpretation more natural, in some sense, than a strictly

Consideration of affinities within the Metatheria involves some decision as to recognition of other natural subordinate taxa within that taxon. It is still true that the largest taxa, or rather those of highest category within the Metatheria, generally accepted as natural evolutionary groups are approximately those I listed in my now old classification (Simpson, 1945) as superfamilies. With the emendations noted, these are:

Didelphoidea (I now include the Borhyaenidae, which clearly arose from didelphids and most of which are not radically divergent.)

Dasyuroidea
Caenolestoidea
Perameloidea
Phalangeroidea

There are aberrant or little-known forms of doubtful status that might eventually also merit superfamily distinction, for example, *Necrolestes* (now in the Didelphoidea), *Notoryctes* (in the Dasyuroidea), *Groeberia* (in the Caenolestoidea), or *Vombatus* and *Tarsipes* (in the Phalangeroidea), but as minimal major groups the five named seem surely to be natural, and the marginal forms that may represent additional major groups do not matter for present purposes. None has any special resemblance to the argyrolagids, with the possible exception of *Groeberia* and *Vombatus*, mentioned below.

These taxa, variously named and ranked, have often been grouped at higher categorical levels, suborders or orders, within

the Metatheria. Classical arrangements, a more recent proposal by Ride (1964), and a new suggestion are as follows:

(As Suborders)		(Suborders)	
Polydactyla	{ Didelphoidea Dasyuroidea Caenolestoidea	Polyprotodonta	{ Didelphoidea Dasyuroidea Perameloidea
Syndactyla	{ Perameloidea Phalangeroidea	Diprotodonta	{ Caenolestoidea Phalangeroidea
Ride, 1964 (As Orders)		Alternative suggestion (Suborders)	
Marsupiacarnivora	{ Didelphoidea ²⁴ Dasyuroidea ²⁴	Hesperometa-theria	{ Didelphoidea Caenolestoidea
Paucituberculata	Caenolestoidea ²⁴	Eometa-theria ²⁵	{ Dasyuroidea Perameloidea Phalangeroidea
Peramelina	Perameloidea ²⁴		{ dea
Diprotodonta	Phalangeroidea ²⁴		

Of these arrangements, I somewhat prefer Ride's. Still another arrangement, taking account of Ride's but different in some important respects, has been based on additional, especially serological evidence by J. A. W. Kirsch. It may be still more acceptable, but it has not yet been published and cannot be discussed here. All of these groupings are decidedly moot, there is no established consensus, and for present purposes, at least, I prefer to discuss affinities in terms of the superfamilies specified above, without reference to suborders or multiple orders.

In these terms, the Perameloidea can be ruled out as possible ancestors or significantly close relatives of the Argyrolagidae. An ancestor of the Perameloidea that could also be an ancestor of the Argyrolagidae would almost certainly be a primitive dasyuroid and not taxonomically a perameloid. Argyrolagids could have evolved from very primitive, probably Cretaceous, didelphoids or dasyuroids, simply because any

mechanical (or supposedly "objective") phenetic interpretation. I do not mean by this remark to deny either the validity of strictly phenetic classification entirely on its own grounds, understood to be devoid of any evolutionary significance, or its great usefulness as evidence and adjunct for evolutionary classification and for functional interpretation (not classification). I only want to point out a striking example in which most biologists will generally prefer the latter alternatives.

²⁴ Ride does not recognize these groups as such, eschewing the superfamily level and dividing Marsupiacarnivora into six, Paucituberculata into three, and Diprotodonta into five families.

²⁵ Reference is to the east, not to the dawn.

or all marsupials could be derived from such primitive sources. Argyrolagids are so different from such a source and so extremely specialized with respect to it that they would have to be placed in a separate superfamily (at least), if that is the extent of their relationship to other marsupials. (I return to this and suggest that such is indeed the case on a later page.) The Argyrolagidae are obviously very unlike any late, or for that matter any known Caenolestoida or Phalangeroida. However, that does not rule out, *prima facie*, derivation from early Caenolestoida, after that group had differentiated from Didelphoidea (or Dasyuroidea), or from early Phalangeroida, after that group had differentiated from Dasyuroidea (or Didelphoidea). Acceptance of one or the other of those views would indicate reference of the Argyrolagidae on one hand to the Caenolestoida or Paucituberculata, on the other to the Phalangeroida or Diprotodonta.

A first point in considering these various possibilities is the resemblance of argyrolagids to the Vombatidae.²⁶ That taxon, aberrant in the Phalangeroida but usually referred there, includes the only known marsupials other than argyrolagids with continuously growing teeth. The wombats further resemble argyrolagids in having fewer than three upper incisors, no canines, and five cheek teeth. P_3^3 are subtriangular and M_{1-4} are bilobed, further as in argyrolagids. However, special resemblances end there. The incisors are different both in number, $\frac{1}{1} \left(\frac{2}{2} \right.$ in argyrolagids) and in functional aspects (more definitely rodentlike in vombatids), and the upper molars are deeply divided on the labial side (not

there divided at all in argyrolagids). The snout is unusually short and does not project anteriorly to the incisors. The orbit is relatively small and anterior. There is a particularly large temporal fossa and a small, not at all globular cranium. The animals are heavily quadrupedal, ambulatory, virtually tailless, and fossorial. Special affinity of argyrolagids and vombatids seems impossible. Any relationship could be, at most, by derivation of both from basic phalangeroids (or diprotodonts), and the limited dental resemblances must have evolved separately in the two groups.

Relationship with the Phalangeroida must next be considered, especially because the only two students who have previously published extensive studies of argyrolagids, L. Kraglievich and Rusconi, agreed in referring them to that group (as Diprotodonta, with caenolestoids excluded). It must be remembered that their knowledge was limited to incomplete lower jaws and that present disagreement is based on much more extensive evidence than was available to them. (My own interpretation of the lower jaws then available was far wider of the mark than theirs.) In the preceding review of previous views on affinities, it was shown that the few characters specified by L. Kraglievich or Rusconi as evidence of phalangeroid affinities are either also present (in some instances more nearly similar) in caenolestoids, or of even wider occurrence, or contradicted by later knowledge. That is still true of the lower jaws and their dentitions: they have no characters suggestive of phalangeroid, as distinct both from caenolestoid and from merely general marsupial, affinities.

Present knowledge of the skulls of argyrolagids, not involved in previous publication, confirms and strengthens that situation. The upper dentition has no resemblance to phalangeroids except for those few to Vombatidae (and not to any other or to primitive phalangeroids) mentioned above and evidently not homologous.

²⁶ "Phascolomidae" in Simpson (1945) and many other studies. That may also be the legal name under the current code. However, it is now fairly well established that the name of the type genus should be taken as *Vombatus* rather than *Phascolomis*.

The lower and upper incisors could be described as literally diprotodont, but as regards the upper incisors, at least, this is a difference from, not a resemblance to, the so-called diprotodont marsupials. The argyrolagid snout resembles those of perameloids and some caenolestoids to a limited extent in being elongate and more or less tubular, but is thereby entirely unlike any phalangeroid. The ear region, with an epitympanic sinus, complete and somewhat inflated bulla, but no extended meatus, is quite different from that usual or probably primitive for phalangeroids. No special character *sui generis*, among the many in the argyrolagid skulls, is hinted at in any known phalangeroid.

The hind foot is also decidedly *sui generis* in argyrolagids, in a way relevant to phalangeroid affinities and practically conclusive against them. In the preceding anatomical section it was shown that the functional metatarsals are almost certainly III and IV and that all others are absent or reduced to functionless vestiges without appended phalanges. As is well known, in all phalangeroids (and perameloids) digits II and III are syndactylous, that is, each is slender, they are enclosed proximally in a common integument, and they function essentially as a single toe. That cannot have been true of argyrolagids. The longest digit in phalangeroids is IV. II and III, together, and V may be of approximately equal length and almost as long as IV, as in most *Phalangeridae* and probably primitive for *Phalangeroidea*. In some more advanced phalangeroids, notably the *Macropodidae*, II-III and V both tend to be reduced, and the foot may become almost (although never quite in living or known fossil forms) monodactylous on IV. In some forms, e.g. *Dendrolagus*, II-III is reduced but V is large (not quite so large as IV), and there is a tendency toward didactyly on IV and V. Didactyly on III and IV has not and really could not have evolved in this group.

It appears that the hind foot of argyro-

lagids could not have arisen from a syndactylous ancestry. On the other hand, in the didactylous groups *Didelphoidea*, *Dasyuroidea*, and *Caenolestoidea*, pedal digits III and IV are commonly subequal, larger than II and V, and quite separate from the latter. The condition in argyrolagids, although far advanced beyond that, could readily have arisen from it.

All recent or known fossil phalangeroids are both syndactylous and diprotodont. It has been a moot question which condition evolved first and which might therefore be taken as a key character in the original differentiation of the taxon. Those are of course the alternatives involved in classifying marsupials in two suborders, *Didactyla* and *Syndactyla* if syndactyly was believed to antedate diprotodonty, but *Polyprotodonta* and *Diprotodonta* if diprotodonty was supposed to antedate syndactyly. But the *Perameloidea* are syndactylous and polyprotodont, whereas the *Caenolestoidea* are didactylous and diprotodont. One should therefore logically conclude either that syndactyly evolved independently in *Perameloidea* and *Phalangeroidea* or that diprotodonty evolved independently in *Caenolestoidea* and *Phalangeroidea*. Or both might be true. Early authors, Thomas (1895) for one of many examples, tended to consider diprotodonty primary, although they were not always clear that this strongly suggested two separate origins of syndactyly. Only a few recent students still maintain that arrangement. Others have argued that syndactyly arose but once, and that diprotodonty, to the extent that it can be considered similar in both groups, arose independently in *Caenolestoidea* and *Phalangeroidea*. That was, for instance, the strong conviction of Wood Jones (e.g., 1923), who included in the argument the statement that, "No didactylous diprotodont marsupial is known," hence implying that the *Caenolestoidea*, so long and so often considered *Diprotodonta*, are not diprotodont at all, even descriptively.

Syndactyly is a very peculiar, anatomically and presumably also genetically complex structure and functional arrangement that is not known ever to have occurred in any marsupials other than Perameloidea and Phalangeroidea and that is practically identical in those two. Diprotodonty, defined as enlargement and procumbency of one pair of lower incisors, is a relatively simple development that has occurred independently in many groups of mammals, from the multituberculates already in the Jurassic through numerous quite distinct Cenozoic placentals. The arrangement is not alike in detail in caenolestoids and phalangeroids. There are, of course, many other characters and considerations to be weighed, but it does seem quite probable that syndactyly is monophyletic in marsupials and that diprotodonty is not. The issue is evaded by my arrangement into marsupial superfamilies and also by Ride's into metatherian orders, but Ride's general morphological and phylogenetic diagrams (especially 1964, figs. 1 and 2) clearly show syndactyly as monophyletic and diprotodonty (he calls it "pseudodiprotodonty" in his Paucituberculata = Caenolestoidea) as polyphyletic. I agree.

That bears on the present problem in two different ways. First, it indicates that the ancestors of the Phalangeroidea, even before that group existed as such and had differentiated from the Perameloidea, were syndactylous. The argyrolagids could not have had syndactylous ancestors; therefore they were not derived from phalangeroids and cannot be referred to or placed as next relations to them. This is safer than most single-character phylogenetic inferences, and it is supported by the absence of any contrary evidence among the many and complex argyrolagid characteristics now known.

The second bearing is that the apparently independent origin of diprotodonty (or of diprotodonty and "pseudodiprotodonty") in at least two quite distinct groups of marsupials lessens the evidential value

of the distantly similar development in argyrolagids. That is all the more true in that the resemblance of the incisors between caenolestoids and phalangeroids is much greater than that between the incisors of argyrolagids and those of either one of those groups.

In fact, the dentition of argyrolagids is so peculiarly specialized, so radically unlike that of any other known marsupials, that it gives no evidence for relationships below the level of Metatheria. The only particular resemblance to Caenolestidae is the enlargement of lower incisors, but these are different in number and form in the two groups and the upper incisors are entirely dissimilar. Among other caenolestoids, the most primitive known polydolopid, *Epidolops ameghinoi* (see Paula Couto, 1952), does have two pairs of strongly procumbent lower incisors, but they are morphologically and functionally unlike those of argyrolagids, and in *Epidolops* the cheek teeth are already well advanced in a line of specialization completely different from that of argyrolagids.

Comparisons with *Caenolestes*²⁷ have been made throughout the anatomical part of this study. Numerous fossil caenolestids are known, but from such incomplete materials as to add little or nothing to possible comparisons. Moreover, most of them, notably the Palaeothentinae and Abderitinae of Sinclair (1906), are decidedly more specialized than the surviving caenolestids in the known parts, and specialized in such ways as to be even less similar to argyrolagids. Noted resem-

²⁷ There are three supposed genera of living caenolestids: *Caenolestes*, with five claimed species; *Lestoros* (usually called *Orolestes*, a pre-occupied name), with one; and *Rhyncholestes*, also with one. I suspect that placing of the "genera" as three species would be a better biological arrangement, but evaluation of the slight taxonomic distinctions is not relevant for present purposes. I have made first-hand comparisons with *Caenolestes* and "*Lestoros*." "*Rhyncholestes*" is evidently neither more nor less comparable.

blances of argyrolagids to caenolestids include:

Presence of a foramen and canal posterior to M_1 .

Presence of a diminutive masseteric foramen.

Generally similar angular and masseteric regions on mandible.

Flattened, horizontal articular surface on mandibular condyle.

Large anterior palatal foramina and large palatal vacuities.

General, globular shape of posterior part of cranium.

Tympanic similar in shape and in relationship to bulla.

Sharp distinction of anterior and posterior caudal vertebrae and similar structures of both.

Proximal end of humerus and entepicondylar foramen similar.

Generally similar femur.

The number of similarities in such a list, which could be lengthened, is superficially impressive, but only superficially. All of the resemblances are rather general, and most of them are in minor, variable, or evolutionarily plastic details. Many are not exclusive to the argyrolagid-caenolestid comparison but occur in a scattered way among other marsupials (e.g., masseteric foramen) or mammals in general (e.g., entepicondylar foramen). Most of them are aspects of functional systems that are otherwise radically unlike those of caenolestids (e.g., the rather similar femora of the two groups articulate with extremely different pelves, and the distal hind leg segments are also extremely different).

The possibility that argyrolagids evolved from ancestral caenolestoids can hardly be ruled out flatly. If, however, that was their origin, the argyrolagids have diverged to an unrecognizable extent, and no character really diagnostic of caenolestoids is evident in them. When lower jaws and dentitions alone were known, basic separation of argyrolagids from caenolestoids

would not have been justified, but the unusually extensive knowledge now at hand not only justifies but, in my opinion, demands such separation.

Two very poorly known taxa of South American marsupials require passing notice at this point: *Necrolestidae* and *Groeberiidae*. *Necrolestes*, previously usually placed in the *Insectivora* and sometimes in the *Edentata*, was finally shown to be a marsupial (Patterson, 1958). It shares with argyrolagids an elongation of the bony snout anterior to the incisors. In all other characters, however, it is extremely different: number and shape of incisors, presence of large, laniary canines, triangular molars, absence of palatal vacuities, absence of a bulla, and generally fossorial habitus, to name a few such characters. Any special relationship to argyrolagids is impossible.

Groeberia minoprioi, (sole known member of the *Groeberiidae*) is known only by an incomplete lower jaw.²⁸ In the original description, Patterson (1952) pointed out some possible resemblances to *Argyrolagus*: enlarged, hypselodont lower incisor with limited enamel and with intra-alveolar part parallel with the median line of the symphysis; subequal molars of similar structure; strong, projecting coronoid process; and absence of masseteric crest. However, Patterson also pointed out that there are differences: the dentition of *Argyrolagus* is less reduced and it is much later in geologic time; the molariform teeth are hypselodont; and the symphysis is unfused and normal in structure. Present greatly increased knowledge of argyrolagids shows that the differences, even in the few characters known in *Groeberia*, are even greater than appeared. Although a buccal subcoronoid crest is present in argyrolagids, the coronoid itself is feebler than in *Groeberia* and probably quite different. A well-developed masseteric crest

²⁸ I have heard of another specimen, but this has not been described and I cannot confirm its existence.

is present in argyrolagids. Patterson was certainly right in concluding that the two groups clearly represent different lines of descent, and there is at present no evidence that they are more nearly related than by being both marsupials. In the present state of knowledge the question is not so much whether the Argyrolagidae are related to the Groeberiidae as whether the latter are especially related to the former, and much the most probable answer is "No."

By the virtual elimination of reasonable alternatives, what remains is the likelihood that the ancestry of the Argyrolagidae separated from other marsupial taxa at a fully basic level in the Marsupialia, among members of the didelphoid or didelphoid-dasyuroid complex. No known member of that complex shows any special resemblance to argyrolagids, and all one can say is that its most primitive members are sufficiently unspecialized that nothing would seem to exclude them from possible ancestry to argyrolagids—or to any other marsupials. As we know only the terminal argyrolagids, there is the possibility that early forms would indicate some more particular links with other marsupials. However, our knowledge of these terminal forms is now excellent, and it does seem to warrant the definite, although negative, step of separating argyrolagids from all other marsupials. In the system I still prefer, that indicates recognition of a superfamily Argyrolagoidea, which at present requires or warrants no definition apart from that of its unique family.

If Ride's (1964) system of dividing the Metatheria into orders were adopted—and there is much to be said for it—the reasonable classification of the argyrolagids would be still more difficult. That is one of the reasons why I still prefer, even if on a "temporary" basis for a generation or two, division of the Marsupialia (and Metatheria) into superfamilies rather than orders or suborders. Distinctive as they are and well-known as they now are, I would be loath to give ordinal rank to this

little group, at least until some stronger evidence of its ancestry is available. I also hesitate to assign it to any of Ride's proposed orders. I have given reasons for not placing it in the orders Paucituberculata, Peramelina, or Diprotodonta, which are other names and ranks for the Caenolestoidae, Perameloidea, and Phalangeroidae, respectively. Like those three groups, the Argyrolagoidea probably evolved from very early members of Ride's Marsupicarnivora, yet they have changed so radically from primitive "marsupicarnivores" and in a direction so unlike any (other?) later members of that group that reference to it would seem anomalous.

One remaining point would be whether the Argyrolagoidea arose from Didelphoidea or Dasyuroidea. Those groups were barely or perhaps not distinguishable in their most primitive forms. They are distinguished mainly because their descendants evolved separately and became so very dissimilar. I see no morphological evidence for considering argyrolagids as closer to one than to the other. However, it is fairly clear that the South American radiation of marsupials arose from Didelphoidea and the Australian from Dasyuroidea, and the known Argyrolagoidea are exclusively South American. Geographic distribution is also evolutionary, and its evidence favors origin from the Didelphoidea.²⁹ Although I think no circularity is really involved in that argument, the question might arise. In any case, the Argyrolagoidea do have zoogeographic significance and have long been considered in that light. I now turn to that aspect of their study.

ZOOGEOGRAPHY

Former views. Both *Microtragulus* and *Argyrolagus* early became involved in zoo-

²⁹ And therefore reference to the Hesperometatheria, if my only half-serious earlier suggestion for ordinal or subordinal classification were adopted.

geographic discussions. Ameghino (1904) gave no zoogeographic inferences in the original publication on *Microtragulus*. In 1906 (p. 344), however, he was explicit and unequivocal that *Microtragulus* indicated the origin of selenodont artiodactyls in South America and spread (in post-Miocene times!) thence to the rest of the world. In 1912 he radically altered that view:

"Among the artiodactyls those that are surely of North American origin are the llamas or camelids and most of the cervids, but some of the latter, such as *Mazama* and certain fossil forms, are of all the more doubtful origin since the smallest and most primitive known selenodont artiodactyl was found at Monte Hermoso. *Microtragulus argentinus* was no larger than a small rat and it cannot be derived from any of the forms that lived in North America. These primitive forms probably reached South America by the Senegal-Guiana bridge."³⁰

That conclusion and the genus itself have usually been ignored, but Castellanos (1934) reacted against Ameghino's last opinion as follows:

"The Senegal-Guiana bridge created by Ameghino did not exist, as I have already indicated in other publications. . . . The mammals of African and European type that Ameghino has coming to South America do not have that character and come from North America. Moreover, the incomplete condition of their remains has lent itself to wrong determinations. Those

³⁰ "Parmi les Artiodactyles ceux qui certainement sont d'origine nordaméricaine ce sont les Lamas ou Camelidés et la plupart des Cervidés, mais quelques uns de ces derniers comme *Mazama*, et certaines formes fossiles sont d'origine d'autant plus douteuse qu'on a trouvé a Monte Hermoso l'Artiodactyle sélénodonte le plus petit et le plus primitif qu'on connaisse. Le *Microtragulus argentinus* n'était pas plus grand qu'un petit rat et on ne peut le faire descendre d'aucune des formes qui ont habité l'Amérique du Nord. Il est probable que ces formes primitives aient pénétré dans l'Amérique du Sud par le pont guayano-sénégaléen."

of *Microtragulus* are not remains of an artiodactyl but of a rodent. . . ."³¹

Ameghino (1904) immediately hailed *Argyrolagus* as indicating a South American origin for the lagomorphs. His definitive statement in 1906, after a page-long review of the question, was that, "In consequence, *Argyrolagus* should be considered as the last representative, and the only one so far known, of a family of rodents³² forming the origin of all the duplicidentate rodents known from all other parts of the earth" (Ameghino, 1906, p. 368).³³ It is here not absolutely explicit that Ameghino considered that ancestral family autochthonous in South America, but there is no real doubt about the implication. That is conclusively borne out by a diagram on the following page (Ameghino, 1906, p. 369), showing the "Rodentia duplicidentata" as arising, at successively remote times, from the "Promysopidae" [= Polydolopidae], Polydolopidae, "Garzoniidae" [= Caenolestidae], and "Microbiotheriidae" [now included in Didelphidae]. As Ameghino believed, and as is still generally accepted, those are all groups autochthonous to South America and unknown from any other region. It is curious that in this family tree, immediately following the discussion of the supposedly crucial place of the *Argyrolagidae*, the latter family does not appear.

³¹ "El puente guayano-senegalense creado por Ameghino no ha existido, habiéndolo manifestado ya en otras publicaciones. . . . Los mamíferos de tipo africano y europeo que Ameghino hace venir a Sud América, no presentan ese carácter y proceden de Norte América; por otra parte, el estado incompleto de los restos se han [sic!] prestado a determinaciones inexactas. Los del **Microtragulus** [boldface in the original] no son de un artiodáctilo sino de un roedor. . . ."

³² Like virtually all zoologists of the time, Ameghino considered the lagomorphs, or Duplicidentata, a suborder of Rodentia.

³³ "Il en résulte qu'*Argyrolagus* doit être considéré comme le dernier représentant, et le seul connu jusqu'à présent, d'une famille de Rongeurs qui constitue la souche de tous les Rongeurs duplicidentés qu'on connaît de toutes les autres régions de la terre."

In accord with Ameghino's views, it should have been inserted between "Rodentia duplicidentata" and "Promysopidae."

Kraglievich (1931) considered *Argyrolagus* a diprotodont marsupial and argued as follows, in part, about its zoogeographic significance:

"Most probable is its [*Argyrolagus*'] derivation from the primitive phalangeroid³⁴ stock and its immigration into Argentine territory toward the end of the Miocene, coming from a region whence the other phalangeroids emigrated to Australia and nearby islands." He then argued that no known Patagonian fossil marsupials could be ancestral to *Argyrolagus*, and continued: "With Patagonia thus excluded as center of origin of *Argyrolagus*, and with even greater reason any other area of America, Africa, Europe, and the Australian region itself, seeing that no animal discovered in those areas can be an ancestor of the one from Monte Hermoso [*Argyrolagus palmeri*], we must perforce refer its origin to a *terra incognita*, perhaps the South Pacific continent, where the primordial phalangeroids could have lived before their radiation, part of them going off in the direction of Australia, and the rest of them to our country [Argentina]. But in that case it is obvious that we must admit a connection of said South Pacific continent with central and northwestern Argentina across Chile (excluding Patagonia) during the Miocene, by which way *Argyrolagus* could have immigrated." The latter point is supported by Kraglievich's description of *A. catamarcensis*, considered ancestral to *A. palmeri*, from Catamarca, a considerable distance northwest of Monte Hermoso. Kraglievich concludes: "This

extraordinary discovery [of *A. catamarcensis*] strengthens the suspicion of a probable western immigration by *Argyrolagus*, which postulates the elongation toward the west of a large part of the South American continent, far beyond its present limits, around the middle of the Tertiary."³⁵

The existence of a South Pacific continent was assumed, and no real reason was given for assigning the origin of phalangeroids, hence also of argyrolagids according to Kraglievich's views, to that hypothetical continent rather than to Australia. The implicit negative argument was hollow, because when Kraglievich wrote, only one surely pre-Pleistocene fossil mammal (*Wynyardia bassiana*) was known from Australia and it was, indeed, a phalangeroid. The exclusion of Patagonia from the presumed migration route rested on slightly better, but still completely negative grounds. I (Simpson, 1932) opposed those zoogeographic views and argued that *Argyrolagus* was probably a native South American, but it was in this connection

³⁵ "Lo más probable es su derivación a partir del primitivo stock falangérido y su inmigración al territorio argentino hacia fines del mioceno, procedente de una región desde la cual los otros falangéridos emigraron hacia Australia e islas adyacentes."

"Excluida así la Patagonia como centro de origen de *Argyrolagus* y con mayor razón cualquier otra comarca de America, Africa, Europa y la misma región australiana, puesto que ningún animal descubierto en ellas puede ser antecesor del de Monte Hermoso, debemos forzadamente relegar su origen a una *terra incognita*, quizá el continente surpacifico, donde pudieron habitar los falangéridos primordiales antes de que irradiaran dirigiéndose rumbo a Australia una parte, y a nuestro país la otra.

"Pero en tal supuesto, es obvio que debemos admitir una conexión de dicho continente con la Argentina centro y nordoccidental a través de Chile (excluyendo la Patagonia) durante el mioceno, por cuya vía pudo inmigrar *Argyrolagus*."

"Este extraordinario descubrimiento robustece la sospecha de una probable inmigración occidental de *Argyrolagus*, que supone la prolongación de una gran parte del continente sudamericano hacia el oeste, mucho mas allá de sus límites actuales, a mediados del terciario. . . ."

³⁴ In writing "falangérido" and "otros falangéridos" Kraglievich did not mean to refer *Argyrolagus* to the Phalangeridae. Immediately before this passage he made clear that he considered the Argyrolagidae a distinct family although rather closely related to the Phalangeridae. I therefore translate "falangérido" as "phalangeroid," not "phalangerid," in this passage.

that I made the unfortunate guess that it might be an aberrant typosphere.

In his first paper on the subject, Rusconi (1933) briefly reviewed Kraglievich's zoogeographic views and concluded: "The paucituberculated marsupials [Caenolestidae] of Patagonia represent a group of mammals that evolved in a different way; and, according to present knowledge, there is no probability of the existence of a link between them and the *Argyrolagus* group. Neither is there any valid evidence that these Pliocene marsupials of Argentina might have come from the Australian region. Therefore it would not be strange if Kraglievich's theory was proved true some day" (original publication in English).

Later, Rusconi (1936, p. 180) raised but did not attempt to answer two questions: "Have the argyrolags, along with marsupials in general, their origin in the Australian region or perhaps in a South Pacific *terra incognita*, now submerged, from which marsupials would have spread before the Cretaceous, some toward Australia and others toward South America? Or might the argyrolags have reached Argentina from the west and by way of lands now submerged but without having passed through Patagonia?"³⁶ These apparent alternatives are not really such. Kraglievich and, following him, Rusconi himself had previously answered both questions affirmatively. In the next paragraph, however, Rusconi may possibly imply that the marsupials, wherever they came from, evolved from earliest times quite separately in Australia and South America, and if that is his meaning it might also imply South American origin of the Argyrolagidae.

However he made no such definite statement, and this whole discussion is so vague that I am uncertain as to whether he had formed a clear opinion or, if so, what it was.

Most recently, Rusconi (1967, p. 284) has been somewhat more positive, reverting to essential agreement with L. Kraglievich. He states that *Argyrolagus*, *Microtagulus* [sic! and here retained as a separate genus although suspected of synonymy], and various Paleocene notoungulates have no known ancestors. He concludes: "Their remote ancestors should sometime be found in those broad lands now buried under thick layers of ice of the Antarctic pole, or else in lands now covered by the South Pacific sea, reckoned so to speak as the *terra incognita*. Surely that is whence will some day be afforded the remains of ancestral lineages, and thereby it will have become possible to make an end of so many interesting arguments arising from the study of ancient life. . . ." ³⁷

The history of study of the affinities and zoogeography of *Microtagulus* and *Argyrolagus* is an appalling mass of inaccuracy, faulty logic, unfounded opinions, and misidentifications. I can say so without snobbery because I contributed something to the confusion. So did one of the greatest authorities on South American mammals W. B. Scott (1937, p. 240): "Of the very numerous Rodentia of the so-called Araucanian stage, only the rabbit († *Argyrolagus*) was an immigrant from the north, all the others belonging to autochthonous families."

Present status. Decision that the Argyrolagidae are not Phalangerioidea or derived

³⁶ "Los argirolagos como los marsupiales en general tienen su origen en la región australiana o bien en una *terra incognita* sur pacífica, hoy submergida, y de la cual habrían irradiado antes del cretáceo marsupiales que se hubieran dirigido: unos hacia Australia y hacia sudamérica otros?, o bien, Los argirolagos habrían llegado a la Argentina por Occidente y por tierras hoy submergidas pero sin haber pasado por la Patagonia?"

³⁷ "Sus remotos antecesores deben ser hallados alguna vez en aquellas extensas tierras sepultadas actualmente por espesas capas de hielo del Polo Antártico, o bien en tierras actualmente cubiertas por el mar Pacífico del Sud, conceptuada en cierto modo como la 'terra incognita'. Seguramente es de donde proporcionarían algún día los restos de ramales precursores, y con ello, se habrá podido dar término a tantas interesantes discusiones que surgen del estudio de la vida pretérita. . . ."

from any separate pre-phalangeroid stock at once removes them from providing any possible evidence for a South American-Australian connection in the Southern Hemisphere, whether directly or through Antarctica or by dispersal from an intermediate *terra incognita*. A detailed review of theories of land connections of South America with Australia, on one side, and Africa, on the other, is not called for in this place, but these may be briefly mentioned.

Marsupials figured largely in the hypothesis of a South American-Australian connection, which long antedated L. Kraglievich's zoogeographic views on argyrolagids and was, indeed, becoming obsolete when he wrote. Some early South American didelphids resemble primitive Australian dasyuroids. Some advanced, not early or primitive, South American borhyaenids resemble the advanced Australian dasyuroid *Thylacinus*. Primitive, not exclusively early but not advanced, South American caenolestoids have characters that could have occurred in hypothetical ancestors of the Australian phalangeroids. It has, however, been cogently argued and is now generally accepted that resemblances in primitive features are in general derived from a didelphoid or didelphoid-dasyuroid complex that was widespread in the northern continents and does not require or suggest a southern connection. Resemblance in more specialized characters is not in any case really detailed or extensive, and is more logically explained by convergence than by homology. For example, it seems beyond serious doubt that the more or less *Thylacinus*-like borhyaenids evolved in South America from didelphids and have no closer connection with *Thylacinus*. (The evidence is summarized, with citations of earlier literature, in Simpson, 1948.)

In suggesting that the argyrolagids indicate a South American-Australian faunal connection L. Kraglievich was thus endorsing a hypothesis long sustained but now

generally rejected. He was advancing ostensibly new evidence and not reinforcing the supposed caenolestoid-phalangeroid relationship, because he believed that the argyrolagids, interpreted as Diprotodonta along with the Phalangeridae and some other Australian families, were not related to the Caenolestidae within the Marsupialia. His assumption that the connection was through a South Pacific continent between Australia and South America involved another hypothesis that had once had some technical support but that has now been quite conclusively disproved and was, indeed, generally abandoned even when Kraglievich (and still more later when Rusconi) wrote.

As far as mammals are concerned, supposed connection between South America and Africa has involved especially primates, rodents, and sirenians, with the occasional more marginal mention of a few other groups such as proboscideans and hyracoids. That supposed evidence is not relevant here beyond noting that a strong consensus now holds that no direct connection exists among the known terrestrial mammals. The African Miocene *Palaeothentoides africanus* (Stromer, 1932) was at first believed by its describer to be not only a marsupial but also a caenolestoid and hence of South American affinities, but Butler and Hopwood (1957) showed that it belongs in the exclusively African placental family Macroscelididae. (See also Patterson, 1965.) Castellanos (1934, quoted above) was of course right in negating Ameghino's claim that *Microtragulus* migrated to South America from Senegal. That arose from Ameghino's inevitable misidentification of the isolated bones on which *Microtragulus* was based. Castellanos's disagreement involved an equally great misidentification, but his geographic disclaimer was correct and present indubitable identification of *Microtragulus* as an argyrolagid marsupial puts a complete negative to any hypothesis of affinities with Africa.

The present situation is that no argyrolagoids and no identifiable argyrolagid ancestors more advanced than the didelphoid or didelphoid-dasyuroid complex ancestral to all other marsupials are known from anywhere but Argentina. Didelphoids were abundant in South America by the late Paleocene, and they, as well as some other marsupials, were then already highly diverse (e.g., Paula Couto, 1962, on didelphids; Simpson, 1948, on other early marsupials). Although no identifiable marsupials older than the probable late Paleocene have yet been found in South America,³⁸ primitive didelphoids, conceivably ancestors of the argyrolagoids, must have been there by the late Cretaceous.

On present evidence, then, the most probable view is that the Argyrolagoidea arose in South America from didelphoid ancestors and are another of the numerous groups both autochthonous and endemic in that continent. The only argument against this, now that diprotodont relationships are ruled out, is one advanced by L. Kraglievich and endorsed by Rusconi. The argyrolagoids, highly characteristic and

extremely specialized, suddenly appear in the middle Pliocene, at the earliest, without members or recognizable ancestors in any earlier South American fauna. However, the conclusion that they were therefore immigrants from a *terra incognita* in the Pliocene does not follow. Even in Patagonia, with the richest record, it is extremely improbable that all groups of small mammals present between Paleocene and Pliocene have yet turned up in collections. Moreover, Patagonia has always been marginal in South America, as it is now. There are enormous areas with little or no fossil record where groups of limited ecological or climatic distribution could have been evolving without entering the known fossil record.

Because there is no impelling likelihood that argyrolagoids were absent from Patagonia and because there are vast areas elsewhere in South America where they could have originated and evolved, on present evidence there is certainly no reason to believe that they immigrated from the west and north of Patagonia.

In summary, argyrolagoids probably originated in South America in late Cretaceous or early Tertiary time and remained endemic to that continent. It is possible but not demonstrable that they evolved for the most part in central (now tropical) South America and spread to the more marginal southern zone from which their remains are known in the late Tertiary. It is highly probable, but again not demonstrable, that they evolved under special ecological conditions poorly sampled by the known fossil record.

Finally, in view of recently revived interest in the theories of continental drift and of Gondwanaland, a remark on those may be added. The evidence of the argyrolagoids agrees with and to that extent reinforces the view that South America had no land connection with either Australia or Africa during the late Mesozoic and Cenozoic. It thus adds a small additional item, of no great significance in

³⁸ Early supposed records of mammals older than late Paleocene were shown long since (Simpson, 1932) either not to be definitely mammalian or not to be of the supposed ages. A subsequent discovery is that of Jurassic tracks believed by Casamiquela (1961) to be mammalian. If mammalian, they are unidentifiable as to subclass or order and cannot be compared with any groups the affinities of which can really be discussed. It is quite likely *a priori* that Jurassic mammals occurred in South America, but even if they were clearly identified, it is improbable that they would cast much light on the direct origins, geographic or taxonomic, of Tertiary taxa and faunas. Jurassic mammals of definite identification are known from North America, Europe, and Africa, and they do not cast much light on the Tertiary mammals of those continents. The only other South American mammal supposedly earlier than late Paleocene recently reported is the possibly Cretaceous *Perutherium* Grambast *et al.* (1967). It is clearly a primitive mammal, but both its age and its affinities are somewhat doubtful. It is almost certainly not a marsupial and evidently has no bearing on the argyrolagids.

itself, to the large body of evidence that Gondwanaland did not exist during those times and that continental drift did not then have any influence on land faunas and has little, if any, bearing on the present distribution of mammals. Whether Gondwanaland or continental drift or both occurred at earlier times and had some bearing on early Mesozoic and still older zoogeography is another matter, not relevant here.

BIOLOGY AND ECOLOGY

Function and convergence. As has become evident in previous pages, the argyrolagids present one of the most striking known examples of evolutionary convergence. Although there are more limited convergent resemblances to some other groups (e.g., to *Vombatus* in the dentition; to small macropodids in limb proportions and inferred locomotion), strongest convergence is with certain rodents: especially the kangaroo rats among the Heteromyidae (Dipodomyinae) and jerboas among the Dipodidae (Euchoreutinae, Allactaginae, and Dipodinae). For classification and figures of skulls and mandibles, see Ellerman (1940). For osteology see Lyon (1901), Hatt (1932), and Howell (1932; although only *Dipodomys* is mentioned in the title, comparisons with jerboas and illustrations of the latter are given throughout). My first-hand comparisons have been mostly with *Dipodomys merriami* and *Allactaga mongolica*. Over all, convergence has been stronger to the jerboas, but some characters are more like those of kangaroo rats.

The resemblance most obvious at first sight is in limb proportions and other characters associated in these living rodents, and therefore also by inference in the argyrolagids, with bipedal, ricochetal locomotion. There are, however, numerous other resemblances. Some of these, as in the masticatory apparatus, likewise can be ascribed with little doubt to similar functional adaptations. Others, such as the

presence of palatal vacuities, have no functional significance evident to me, at least. They may, of course, have a common adaptive basis that I have failed to identify, or some may be coincidental, that is, may not have arisen by convergent adaptation to similar functions. There are nevertheless far too many resemblances to be entirely or to any great extent coincidental. Argyrolagids and the placental rodents toward which they converge (or which converge toward them) are only very distantly related and certainly had quite different ancestors. A common genetic basis, beyond that present in all Cenozoic Theria, cannot be involved; that is, this is a case in which convergence and parallelism can be clearly separated and the latter is ruled out. The resemblance between the kangaroo rats and the jerboas, here, incidentally involved, seems also to be largely convergent, but since both groups are rodents and probably had a common ancestor as late as the Eocene, a minor element of parallelism, i.e., of common genetic base for their specializations, may also be present.

In the dentition, resemblance of the argyrolagids is hardly more specific than to rodents in general: gnawing incisors; reduction of incisors, loss of canines, and reduction of premolars with development of a diastema; a grinding battery of a closed series of cheek teeth. The numbers of incisors and of cheek teeth are different. The cheek teeth resemble those of kangaroo rats in being rootless and wearing as quite simple prisms. Jerboas do develop somewhat heightened crowns but their teeth are rooted, subhypsodont at most, and somewhat, although not very much, more complex in pattern. The convergence here is just that the animals in question all have gnawing-grinding dentitions.

All three groups have rather long, narrow snouts. That is most marked in argyrolagids and resemblance is more to kangaroo rats than to jerboas. In argyrolagids the bony snout projects as a closed tube well in advance of the incisors; in *Dipo-*

domys it also projects well, but less than in argyrolagids, and it is open ventrally; in *Euchoreutes* it projects only slightly, and in *Allactaga* not at all. In *Allactaga* the incisive foramina are even larger and especially longer, proportionately, than in *Argyrolagus*. It is quite extraordinary that jerboas are among the few placentals that have palatal vacuities, quite large in *Euchoreutes*, for example (see Ellerman, 1940, fig. 150). They are even larger in *Argyrolagus*, but this is a convergent resemblance, and a baffling one. Such vacuities may be primitive for marsupials, but they have often been lost in that group; examples in South America are the Borhyaenidae, Necrolestidae, and some Caenolestoidea. These vacuities are not primitive for placentals and certainly evolved independently in the jerboas.

The remarkable orbital structure was stressed in the preceding anatomical description of *Argyrolagus* and some descriptive comparison was made with *Dipodomys*. The functional aspects can here be considered further and comparisons made with jerboas. In both kangaroo rats and jerboas the large eyeball is relatively posterior and does not fill the anterior part of the orbit. A temporal fossa is hardly distinguishable as such. These characters are carried to an extreme in *Argyrolagus*. In both of the recent groups the temporal muscle is greatly reduced and has a small origin, not on the cranium above the ear but almost on the posterior rim of the orbit. That must also have been true in *Argyrolagus*. In both kangaroo rats and jerboas the coronoid process on the mandible is correspondingly reduced, short anteroposteriorly and low vertically. It is likewise short in *Argyrolagus* and, although its height is not known, it must have been low, as inferred not only from analogy but also from the manifestly weak temporalis muscle and the lack of room posterior to the orbit.

The functional convergences in the anterior part of the orbit, although less

obvious, are perhaps even more unusual. It has already been noted that the anterior part of the orbit is partly enclosed by bone dorsolaterally in *Dipodomys* and that a deep slip of the masseter originates here. In jerboas a much larger deep slip (or *masseter profundus*) originates anterior to the orbit proper and passes to insertion on the mandible posteroventrally through the greatly enlarged infraorbital foramen. In *Argyrolagus* almost exactly the same functional arrangement, correlated with reduction of postorbital jaw musculature and relatively posterior position of the eyeball, has evolved by expansion of the origin of a deep masseter *within* the orbit rather than through the infraorbital foramen. The position of that origin on the skull, the relative mass of the muscle, and its direction of pull on the mandible are similar in *Argyrolagus* and *Allactaga*. If one imagines the musculature unchanged in *Allactaga* but the infraorbital canal remaining primitive, the facial bones therefore covering the origin of the deep masseter, the resemblance to *Argyrolagus* would be very close.

All three of the groups here compared have rather short, broad, globular crania. All have epitympanic sinuses, probably in the mastoid in all three, and all have complete globular bullae, not homologous but functionally similar in *Argyrolagus* and the two groups of rodents. The extension or inflation of these cavities reaches great extremes in *Dipodomys* and some of the jerboas, e.g., *Scirtopoda*. It is moderate and closely similar in *Allactaga* and *Argyrolagus*. As has often been noted, the tendency for development and inflation of tympanic sinuses in recent mammals, mostly rodents, is especially common in arid and semiarid regions, although not confined to them. There has been long discussion of this point, some of it highly speculative but recently involving detailed experimentation and analysis. Webster (1961, 1962) has demonstrated for *Dipodomys* that the large middle-ear volume reduces damping

in the transmission of vibrations to the middle ear, produces resonance, and increases sensitivity to particular resonant frequencies. There is some evidence that the same effect occurs in *Meriones* (Legoux and Wisner, 1955), and it seems probable that it is general.

As far as I know, there are no data on the point, if any, at which middle-ear inflation becomes effective in producing resonance, and it is therefore uncertain whether this is an adequate explanation for the moderate inflation in *Argyrolagus*. A reasonable hypothesis might be that any development of a bulla (or hypotympanic sinus), an epitympanic sinus, or both, increases resonance proportionately and also is involved in the placing and height of peaks of sensitivity, in tuning the ear, so to speak. There would then presumably be an optimum degree of resonance and of flattening, peaking, and range of response toward which natural selection would bear in any given ecological situation.

For further understanding it would be necessary to know the adaptive significance of specific peak sensitivities, where these occur. Legoux, Petter, and Wisner (1954) suggested that in *Meriones* adaptation is for sensitivity to the cries of other individuals of the same species, thus promoting breeding in sparse, widely scattered populations. However, they presented no evidence that this does in fact occur. Webster (1962) has indicated that in *Dipodomys* intraspecific calls do not in fact occur in the range of most acute hearing. He demonstrated that auditory sensitivity in *Dipodomys* is crucial in evading predation in the dark by owls and rattlesnakes, which are in fact principal nocturnal predators on these rodents in nature. It does not follow that middle-ear inflation is always related to sounds produced by predators, but this is the only relationship that can now be considered definitely established. It also supports the more general proposition that inflated ears are tuned to a

range in which there are environmental signals that affect survival of individuals or of species. (The facilitation of mating, if it occurs, would be within this category.)

Most recent mammals noteworthy for middle-ear expansion are also bipedal. An example additional to various rodents is provided by the elephant shrews (Macroscelididae). It has been suggested that ear specialization is related to equilibrium in these animals, but Webster's studies negate this. Nevertheless a relationship to ricochetal locomotion is indicated. Audition triggers an immediate leap into the air, and in Webster's experiments this was highly successful in thwarting the strike of a predator. Bartholomew and Caswell (1951) also noted it as the usual startle reaction in *Dipodomys*. Thus the two quite different morphological specializations are involved in a single behavioral adaptation. Although this has so far been demonstrated only for *Dipodomys*, it is a reasonable hypothesis, in the absence of evidence to the contrary, that it is also true of other saltatory mammals with expanded middle-ear cavities, including *Argyrolagus*. It is also relevant that most recent animals of this habitus are nocturnal or crepuscular. Although they tend to have large eyes with good light-gathering capacity, as did *Argyrolagus*, that habit would place a premium on audition as part of their defense mechanisms.⁵⁹

⁵⁹ Although beside the present point, it may be of interest as a passing note that practically all early and the smaller later notoungulates, which were long the most abundant South American mammals, had notably expanded middle-ear cavities, with large epitympanic sinuses and bullae. In larger species these are not correspondingly enlarged but are relatively small although still present. These animals, even the small ones with proportionately enormous middle ears, were not bipedal but were cursorial. It is unlikely that their environments were arid or semiarid as a rule. It is also unlikely that many, if any, were nocturnal. They were evidently subject to heavy attack by a variety of predators, including large snakes. The large species must have been under less predation pressure.

In argyrolagids, kangaroo rats, and jerboas it is part of the bipedal adaptation that the pose of the head, indicated by the foramen magnum, condyles, and atlas, was at a marked angle to the neck.

In all three groups the symphysis of the mandible is unfused. All have reduced coronoid processes, as already noted. In *Argyrolagus* and jerboas, but not so much in kangaroo rats, the condyle (and correspondingly the glenoid surface on the skull) is little elevated above the level of the alveolar rim. In all there is a foramen and canal posterolateral to the last molar on the medial side of the anterior part of the base of the coronoid process. In *Allactaga* there are several openings in this area and another piercing the jaw posterior to the coronoid; this is not present in *Argyrolagus* or *Dipodomys*. Jerboas have a large, sometimes double masseteric foramen or vacuity in the mandible, somewhat similar to that of some phalangeroids. This is a verbal resemblance to *Argyrolagus*, but it is improbable that the small foramen of that genus is functionally similar. *Argyrolagus* has a fairly typical marsupial angular region and this does differ notably from that of generally convergent rodents. There is, however, some functional resemblance in the peculiar angular region of *Dipodomys*, in which the angle proper is strongly everted, somewhat like the masseteric crest of *Argyrolagus*, but also has a strongly inflected flange, somewhat like the angular process of *Argyrolagus* and most other marsupials.

Unfortunately, except for the not especially distinctive atlas we have no presacral vertebrae of *Argyrolagus* to compare with the columns of ricochetal rodents (see Hatt, 1932). *Argyrolagus*, *Dipodomys*, and *Allactaga* all have two similar fused sacral vertebrae entering into the sacroiliac joint, but in the last two there are two more fused sacrals or pseudosacrals posterior to those, and in *Argyrolagus* there are not. All three genera have very long and heavy tails, further similar in that proximal

caudals with short centra, transverse processes, and traces, at least, of neural arches are abruptly followed by vertebrae with very long centra and no transverse processes or arches. Tails of this sort are an essential part of ricochetal adaptation, although, as has been noted, some evidently non-ricochetal forms, such as *Caenolestes*, have similar tails.⁴⁰

Too little is known of the scapula of *Argyrolagus* for significant comparison. As noted in the anatomical section, the pelvis is markedly different from that of *Caenolestes*. It is functionally similar to those of *Dipodomys* and *Allactaga*, especially the latter, which it more nearly resembles in the larger angle between the pubis and the ilium and in the larger symphysis, nearly parallel to the iliac-ischiac axis.⁴¹ As pointed out in the anatomical section and shown in Table 3, the presacral extension of the ilium or, correspondingly, the relative approximation of acetabulum and sacrum seems to be a character of these bipedal ricochetal forms and is similar in kangaroo rats, jerboas, and *Argyrolagus*, but extreme in the latter.

Some limb measurements and proportions are given in Table 4 (p. 68). Most significant are the proportions there indicated by the ratios A/C and $(A+B)/(C+D)$. Those show that in *Argyrolagus* and the bipedal ricochetal macropodids and rodents compared the humerus is less than half as long as the femur. The discrepancy in the second segments, ulnae and tibiae, is even greater. The great reduction in size of the

⁴⁰ I have not found a direct observation of locomotion in living caenolestids. Although their limb proportions and structures evidently exclude habitual bipedalism or ricocheting, it is entirely possible that they are effective hoppers.

⁴¹ The specimen of *Allactaga mongolica* that I have used for most of these comparisons, Amer. Mus. Nat. Hist. No. 55978, male from "Ussuk," Mongolia, differs noticeably from that ascribed to the same species figured by Howell (1932, fig. 15A), but the differences in detail do not seem important for the present functional comparisons of distantly related animals.

foreleg and great increase in size of the hindleg would in itself force the conclusion that *Argyrolagus* was bipedal-ricochetal. It is true that the Australian dasyurid *Antechinomys*, which had for generations been described as bipedal because of the discrepant lengths of its fore and hind legs, has recently been shown by Ride (1965) to be quadrupedal with a true, but quite peculiar, gallop as its fast gait. That is, however, an exceptional case, and the over-all resemblance of *Argyrolagus* to the ricochetel rodents is closer than its resemblance to *Antechinomys*.⁴² It is also of interest that Bartholomew and Caswell (1951) found that a species of *Dipodomys*, *D. panamintinus*, with a completely bipedal fast gait, also habitually uses a quadrupedal slow gait somewhat similar to the quadrupedal fast gallop of *Antechinomys*. (Compare Bartholomew and Caswell, 1951, fig. 1, especially 1F, with Ride, 1965, fig. 1, especially 1.5.) Those authors found that another species of kangaroo rat, *D. merriami*, living in the same area is habitually bipedal even when moving slowly and rarely uses its forelegs in walking.

The ratio of humerus to radius in *Argyrolagus* is approximately as in recent caenolestids. In the macropodids and rodents compared the radius is relatively more elongated, but the difference is so little that it may have no functional significance. (Also note that these figures are estimates from incomplete bones, not precise measurements, in *Argyrolagus*.)

The humeri are generally similar in the three groups here especially compared, but *Dipodomys* and *Allactaga* both have the distal end of the deltoid crest produced into a strong tubercle, sharper and more definite than in *Argyrolagus*. The supi-

nator ridge is somewhat higher and more flared in *Argyrolagus*. The humerus of *Argyrolagus* resembles that of *Dipodomys* in having an entepicondylar foramen and that of *Allactaga* in having a supratrochlear foramen. Radius and ulna are generally similar in form in the three genera.

Osgood (1921, p. 95) has shown that the tibia is longer relative to the femur in *Caenolestes* than in any other quadrupedal marsupial with which he compared it. The only strictly bipedal form compared was *Macropus giganteus*. As shown in Table 4, the most extremely bipedal of the recent forms compared, jerboas, have the tibia somewhat less elongate than the others, but the differences are hardly significant. Elongation is generally greater in bipeds, including *Argyrolagus*, than in quadrupeds, but the caenolestids are among a number of exceptions in the latter groups. It is somewhat unexpected that the metatarsus is not unusually elongated in at least some small macropodids. It is decidedly elongated in *Argyrolagus*, kangaroo rats, and jerboas. Elongation within the tarsal bones, which evolved at least three times independently in saltatory prosimians, is absent in this habitus (that is, the adaptive facies of *Argyrolagus* and its placental analogues).

The femora are generally similar in the three groups, but there are some differences the adaptive significance of which is not clear. The head, neck, and greater and lesser trochanters are functionally similar, and all have a strong, deep digital fossa, but in *Dipodomys* and *Allactaga* this extends obliquely to the base of the lesser trochanter and in *Argyrolagus* it extends straight distally, not near that base. *Argyrolagus* and *Dipodomys* have, but *Allactaga* lacks, a third trochanter. That of *Argyrolagus* is less sharp and produced, more proximal than that of *Dipodomys*. One would suppose that these differences would effect locomotion, but the bearing is not known and Howell (1932, p. 523) states in a categorical but, to me, somewhat puzz-

⁴² The Australian placental rodent (murid) *Notomys* is indeed bipedal-ricochetal (confirmed by Ride in the same brief published note) and is another of the numerous instances of association of that kind of locomotion with an inflated middle ear and an arid habitat.

zling way that the absence of a third trochanter in jerboas (and *Pedetes*) "has nothing to do with saltation."

The tibia and fibula are closely similar in all three groups, with no distinctions among these three of probable functional significance. Their great length and their fusion are saltatory specializations.

The development of a true or pseudocannon bone is among the most striking features of the convergence, and especially interesting and characteristic of convergence from widely different ancestries in that it indicates close similarity in functional adaptation but is not morphologically homologous. In *Argyrolagus*, as described earlier, the pseudocannon bone consists of metatarsals III-IV and there are no other functional toes. In jerboas (except *Euchoreutes*) there is a triple cannon bone consisting of fused metatarsals II-III-IV. *Allactaga* generally retains digits I and V, but they are slender, short, and hardly functional. In *Dipus* and its closer relatives the lateral digits are completely suppressed, as in *Argyrolagus*.

Ecology. The convergences now discussed are so close and extensive that they must indicate similarities in adaptation and way of life, although doubts remain as to just how far such inferences can be carried. Several distinct but adaptively related functional systems are involved, especially: dentition and mastication, vision, hearing, and locomotion. Argyrolagid food habits were rodentlike and more specifically probably included mainly seeds and other nutritious parts of plants, and probably some insects, as is true of the most nearly similar living rodents. The large eyes, and indeed also the general habitus, suggest nocturnal and crepuscular activity. Auditory acuity was at least on the level of *Allactaga* but probably less peaked and less specialized for low frequencies than in most kangaroo rats. Locomotion was normally bipedal, although a facultative slow quadrupedal gait is not excluded; it was probably ricochet at top

speed; and it probably included a saltatory startle and defense reaction.

All living animals of this general adaptive type have ranges in semiarid to arid regions, although a few spread also into areas of greater rainfall and more vegetation, especially grasslands. Bartholomew and Caswell (1951) summarize the ecology of *Dipodomys* in part as follows:

"Except in a few instances the genus *Dipodomys* inhabits regions characterized by a lack of continuous plant cover. . . . The problem of escaping predators is not one of sustained high-speed locomotion, but one of quick-starting evasive locomotion in open terrain over short distances. . . . This rodent can be expected to occupy successfully only those regions in which smooth-surfaced, sparsely-vegetated foraging areas are available. These areas need not, however, be extensive."

It is a further element of this adaptive system that the animals live in burrows and have a restricted feeding range, mainly across open ground, around the burrow. Similar habits are reported for jerboas (e.g., Feniuk and Kazantzeva, 1937).

Recent rodents of this habitus also have some striking physiological adaptations. For example, kangaroo rats and jerboas can live indefinitely without drinking and have highly concentrated urine. (See Schmidt-Nielsen, 1964, for these and other physiological adaptations.) It would be carrying serious paleobiological inference too far to assume that argyrolagids had similar physiological adaptations to arid environments, but it is an interesting speculation.

The faunal associations of argyrolagids give some additional evidence as to ecology. The Chapadmalal Formation, as restricted, has relatively abundant argyrolagids (they are everywhere far from absolute abundance) and has a rich, adequately identified, definitely associated fauna, listed by Reig (1958). The fauna suggests a predominance of open grassland.

There was certainly abundant food for grazers and browsers. Truly arid or desert conditions seem to be ruled out, but semi-arid conditions, relatively open and with some bare soil, more or less as in the southern pampas and much of Patagonia today, are quite possible. There are no definitely arboreal animals, although a few, such as the fairly common didelphids, could possibly have been arboreal. The predominant faunal elements are edentates and rodents, consistent with semiarid grassland and brushland (*pampa* and *mata*). The less common ungulates include probable browsers and grazers, as well as a peccary (*Platygonus*). Recent peccaries are remarkably eurytopic and eurykous, ranging from the equator far into the Temperate zones and from rain forest to full desert, and the Chapadmalal ungulates (as well as some other mammals) may well have been also. The presence of fairly common remains of leptodactylid frogs and of capybaras, and indeed also of so many other animals, indicates the presence of water, probably but not necessarily perennial streams.

Other faunas associated with argyrolagids are not so well documented, and at Monte Hermoso and in Catamarca the precision of association is uncertain. However, the probable associations and ecologies are generally similar to those in the Chapadmalal Formation. Rather cursory studies of sedimentation do not as yet add significantly to the ecological picture.

There is a fair probability that the principal peculiarities of the argyrolagids evolved as adaptations under desert conditions. If so, their known occurrences are in ecologies still appropriate for them but probably less extreme than the ancestral environments primarily responsible for their specializations or marginal to those environments. Ancestral stenokly in localized environments little or not represented in the known fossil record could also bear on the late appearance of this group in

that record and its appearance in already fully specialized form.⁴³

Extinction. It is well-known that extinction rates of mammals throughout the world were high in the Pleistocene and immediate post-Pleistocene. It has further often been pointed out that in this episode large mammals were much more liable to extinction than small. Innumerable causes for those extinctions and for the size differential have been postulated. Gill (1955), referring to Australian marsupials, suggested that although some concomitants of gigantism had a powerful effect, it was not the sole cause, that each case of extinction must be judged separately, that causes were multiple, and that they included psychological and physiological characters not now determinable. Martin (1958, 1966) believes that the primary cause was human predation, with overkill on the larger species. Axelrod (1967) has returned to the classical theory, which dates back at least to Lyell early in the nineteenth century, that the primary cause was change in climate, especially, in Axelrod's form of the theory, as increasingly inequable climates affected reproduction, vegetation, and other ecological necessities.⁴⁴ He supposes that small mammals survived because they had protected homes, stored food, and mated in spring.

The Argyrolagoidea present an extraordinary exception in that a whole major group of quite small mammals became extinct during the Pleistocene. By all rules of analogy and theories of extinction, they should have survived, as did their close ecological analogues in North America, Asia, Africa, and Australia. They cannot be brought under any theory of differential extinction more explicit than Gill's view that extinction of some of the argyr-

⁴³ For a general discussion of stenokly and eurokly see Allee, Park, Emerson, Park, and Schmidt (1949), especially pp. 206-215.

⁴⁴ Note a misprint in Axelrod's paper important to his thesis. Page 32, line 4, for "equability" read "inequability."

olagids' distant relatives in Australia had a combination of causes some of which are unknowable. The case is made more striking by these facts: no other adaptively or ecologically similar animals survived (or ever occurred) in South America, as far as we know; the abundant adaptively and ecologically similar pocket mice and kangaroo rats of North America never spread into South America or competed with the argyrolagids; and South America still has habitats and communities ecologically similar to those in which adaptive analogues of the argyrolagids survived and are still abundant on other continents.⁴⁵

If local arid-semiarid areas ecologically suitable for argyrolagids had gone through a geologically brief episode of greater precipitation, and especially if they had become forested even for a century or so, the resident argyrolagids would have become maladapted and probably extinct. There is, however, no evidence known to me that such an episode occurred.

CONSPECTUS OF SOUTH AMERICAN MARSUPIALS

New knowledge of the argyrolagids emphasizes and extends the evidence that adaptive radiation of marsupials in South America has been even more extensive than is usually realized.

Historical note. Following, with modification, an earlier concept of T. H. Huxley's, Ameghino considered Metatheria (Marsupialia) and Eutheria (Placentalia) as successive evolutionary levels or grades, not as phylogenetic clades (in later nomenclature). Those groups therefore do not appear as taxa in Ameghino's developed classifications. The vernacular term "marsupial" (in French or Spanish) was used, but mostly in a sense descriptive of sup-

posed earlier stages in the ancestry of placentals. Ameghino's classification of 1906 placed what we now classify as fossil South American marsupials in eight major taxa (mainly orders, although the categorical level is not always clear): Allotheria, Paucituberculata, Pedimana, Insectivora, Sparassodonta, Creodonta, Prosimiae, and Protungulata. Within these, 17 families were based on forms now considered marsupial, and marsupials were erroneously referred to four non-marsupial families. In addition, one family (Odontomysopidae) was placed in association with marsupials but was based on specimens of unidentifiable affinities. Ameghino believed that most placentals were derived independently from one or another of these families, specifying insectivores, carnivores, lagomorphs, rodents, ungulates, and primates.

Even early while Ameghino was working, it was realized by others that many of the groups here in question were marsupials in a phylogenetic sense and not stages in the ancestries of various placentals. Thus in his pioneering textbook Smith Woodward (1898) indicated that Ameghino's four families of Paucituberculata represent one or more families of Marsupialia. He also commented on the "very remarkable" resemblance of Ameghino's Sparassodonta (eventually with 6 families) to the carnivorous marsupials of Australia, but referred them to the suborder Creodonta of the placental order Carnivora.

The major clarification was made by Sinclair (1906) in a monograph coincidentally published at almost the same time as Ameghino's main synthesis of Argentine faunas and mammalian phylogeny. Sinclair showed that almost all the mid-Tertiary (Santacrucian) representatives of Ameghino's numerous orders and families referred to above belong to just three natural groups, each referable to a single family: Ameghino's Sparassodonta, placed by Sinclair in an Australian family (or, as I prefer, subfamily) with *Thylacinus* but now always given family distinction as

⁴⁵ Because there is no apparent reason why argyrolagids should be extinct, the thought arises that perhaps they are not. However, collection of even small, obscure mammals in South America is now so intensive that this is a forlorn hope.

Borhyaenidae; Ameghino's Paucituberculata, placed in the Caenolestidae; and Ameghino's Pedimana, placed in the "Didelphyidae" (i.e., Didelphidae).

Genera referred by Ameghino to the Allotheria, absent from the middle (and later) Tertiary and not considered by Sinclair, were later shown to represent a single distinctive marsupial family, Polydolopidae, allied to the Caenolestidae (Gregory, 1910; Simpson, 1928, 1948). The situation has further been tidied up bit by bit by showing that various others of Ameghino's marsupial, or supposedly marsupial-like, taxa either are invalid or belong in one or the other of the four families so far indicated: Didelphidae, Borhyaenidae, Caenolestidae, and Polydolopidae. The Caroloameghiniidae, referred by Ameghino to the Protungulata, are closely related to the opossums (Scott, 1937; Simpson, 1948), and I would now place them as a subfamily of Didelphidae.⁴⁶ As noted above, the "Odontomysopidae," placed by Ameghino in the Allotheria, are unidentifiable, probably not marsupials (Simpson, 1967). *Anisodolops*, placed by Ameghino in the multituberculate family Neoplagiaulacidae, is a synonym of *Polydolops* and of course belongs in the Polydolopidae (Simpson, 1948). *Argyrolestes* and *Nemolestes*, placed by Ameghino in the Jurassic family Spalacotheriidae, which he erroneously considered Insectivora, belong in the Borhyaenidae (Simpson, 1948). In Ameghino's Prosimiae, the Clenialitidae and *Pitheculites*, referred to the Homunculidae (which are Primates), are *incertae sedis* but could belong to the Caenolestidae (Bluntschli, 1931). Sinclair (1906) had already shown that *Acrocyon*, referred by Ameghino to the Creodonta, belonged in the vicinity of *Borhyaena*, hence in the Borhyaenidae of current classifications.

Thus almost all of Ameghino's taxonomy was cleared up, and considerations of

marsupial evolution in South America have generally been in terms of the four families specified above that are, so to speak, residual from Ameghino's classification. However, Patterson (1958) has shown that the Necrolestidae, sole genus *Necrolestes*, referred by Ameghino, Scott, and others to the Insectivora, are a highly distinctive, valid family of Marsupialia, and Patterson (1952) also added another very distinctive family, Groeberiidae, based on a specimen found after Ameghino. The situation has been further modified by important discoveries belonging to known families: the extremely distinctive subfamily Thylacosmilinae, family Borhyaenidae (Riggs, 1934); a polydolopid and remarkably varied Paleocene didelphids in Brazil (Paula Couto, 1952, 1962); and the argyrolagids described in this contribution. Less extraordinary but also adding significantly to the total knowledge of South American marsupials have been many other finds and studies, too numerous to specify here; Reig (1958b) and Ringuelet (1953) may be mentioned as examples.

Review of known groups. The supergeneric taxa⁴⁷ now recognized and their known geologic range in South America are as follows:

Didelphoidea

Didelphidae

Didelphinae. Late Paleocene—Recent.

Caroloameghiniinae. Early Eocene.

Sparassocyninae. Middle Pliocene—Early Pleistocene.

Borhyaenidae

Borhyaeninae. Late Paleocene—Pleistocene.

⁴⁷ No engagement is given that any of these family-group names are valid under the present code, and some probably are not. They are, however, the names usual, practically universal, in recent literature and most readily understood by any present student of marsupials or mammals in general. The very extensive, unproductive bibliographic labor that would be necessary to determine the names most likely to be valid is not part of the present research plan.

⁴⁶ In agreement with Clemens (1966), a conclusion I had independently reached but not published.

- Thylacosmilinae. Pliocene—Early Pleistocene.
- Necrolestidae. Early Miocene.
- Caenolestoidae
 - Caenolestidae
 - Caenolestinae. ?Early Eocene—Recent.
 - Palaeothentinae. Early Oligocene—Early Miocene.
 - Abderitinae. Early Oligocene—Early Miocene.
 - Polydolopidae. Late Paleocene—Early Eocene.
 - Groeberiidae. Early Oligocene.
- Argyrolagoidea
 - Argyrolagidae. Late (?Middle) Pliocene—Early (?Middle) Pleistocene.

There are still a few South American fossils, more or less definable at lower taxonomic levels, that are of uncertain supergeneric affinities and might prove to be marsupials. Perhaps the most likely of these is *Gashternia* Simpson, 1935 (see Simpson, 1948, p. 69; Clemens, 1966, p. 33).

The recognized families and subfamilies, with the sole exception of Didelphidae, Didelphinae, are known only from South America. They almost certainly originated on that continent and probably have always been endemic there. Didelphinae are also known from the late Cretaceous of North America and the Paleocene to Miocene of North America and Europe. They reappeared in the Pleistocene of North America, apparently as immigrants from South America, and although they are the most primitive of all known marsupials, they survive on both continents. There is no direct evidence as to where they originated and South America is not ruled out, but indirect evidence makes origin somewhere in Holarctica seem more probable. Early didelphines were probably ancestral to all other South American marsupials. No identifiable marsupials earlier than the late Paleocene have yet been found in South America, but the already marked

differentiation of marsupials at that time implies long post-didelphine evolution. Didelphines, wherever they came from, were almost certainly already present in South America in the late Cretaceous.

Forms transitional between didelphines and borhyaenines were still present in the late Paleocene, although some primitive borhyaenines were also already in existence. In no other case are intermediates between ancestral didelphines and more specialized subfamilies or families known. In each instance, including even the more specialized subfamilies of Didelphidae and Borhyaenidae, the advanced groups appear in the record with their essential specializations already present. It is also noteworthy that most of the specialized groups have short records, although they must have been in existence over much longer periods of time. The Caroloameghiniinae, Necrolestidae, and Groeberiidae are each known from only one geological formation. The Sparassocyninae, Thylacosmilinae, Polydolopidae, and Argyrolagidae are each known from only two or three successive formations or ages, with known spans shorter than an epoch.

Those facts emphasize the incompleteness of the South American fossil record in general. They also suggest that major parts of marsupial evolution were occurring in areas and facies inadequately sampled, if at all, by the known fossil deposits and the collections so far made. In fact before the middle to late Pleistocene most of the faunas reasonably well known are from quite restricted areas for any one age, many such areas are marginal on the continent, and some, at least, of the faunas are of peculiar and limited facies. Didelphidae are quite rare or absent in most known local faunas, but happen to be dominant faunal elements at Itaborai (late Paleocene, Brazil) and in Bed 9 of the Chapadmalal Formation (early Pleistocene, Argentina, also an argyrolagid facies). Groeberiidae are known from only one small exposure and in a very peculiar

faunal facies (see Simpson, Minoprio, and Patterson, 1962). A complete record of South American marsupials would certainly include a large number of taxa, probably some of high categorical rank, now unknown.

Although the radiation of marsupials in South America was doubtless more extensive than is yet known, the radiation demonstrated by the incomplete record is impressive. It is only a little less extensive than the radiation in Australia, and in that respect South America was also a land of marsupials. Convergence and parallelism between the two radiations did occur, but there are also some striking differences. The South American groups will be briefly characterized under family headings.

DIDELPHIDAE. This family is defined to include a large number of genera and species which, although very diverse, did not diverge so much from primitive marsupial morphology as to require higher categorical rank. The family is thus conservative by definition, but the fact that even now in the Recent there are taxa fulfilling that definition indicates remarkable conservatism and low evolutionary rate.⁴⁸ The family as a whole is omnivorous and individuals are usually highly adaptable (or eurykous in ecological terms), but some species and individuals have more limited diets and habits. Many of the smaller South American species probably had more or less insectivore-like habits. (The only member of the Insectivora known ever to have occurred in South America is a recent immigrant in the far north.) Among the already highly varied, yet not markedly different, late Paleocene didelphids in the Itaborai Paleocene is

Derorhynchus, especially insectivore-like, with a long symphyseal region and procumbent incisors and canine. In connection with it, Paula Couto remarked, "It seems to us, then, that the insectivorous didelphids along with the Caenolestoidea as a whole played the same role as the Insectivora in South America Tertiary ecology, as is true of the recent *Caenolestes*" (Paula Couto, 1962, p. 147).⁴⁹ It is probable that some of those Paleocene genera, when better known, will already justify subfamily separation. However, in view of didelphid diversity, I do not now, as formerly, distinguish the microbiotheres at that level. They are more like didelphines than the subfamilies clearly requiring designation as such. In South America, the latter are the early *Caroloameghiniinae* (Simpson, 1948), *bunodont* and *multicuspid*, and the later *Sparassocyninae*, peculiar for short, heavy skulls with epitympanic sinuses and somewhat specialized dentition (Reig, 1958b).⁵⁰

BORHYAENIDAE. For unknown reasons, subject to speculation and hypothesizing

⁴⁹ "Nos parece, pues, que los didelfídeos insectívoros, juntamente con los Caenolestoidea en general, desempeñaron el mismo papel que los Insectivora en la ecología del Terciario sudamericano, como sucede con los actuales *Caenolestes*." It may be added that recent caenolestids are confined to limited Andean areas and that the roles of Insectivora in most parts of South America are now played by small didelphids and some small rodents.

⁵⁰ The Cretaceous didelphoids from North America show a degree, although only in part a kind, of diversity comparable to that now known for Paleocene-Eocene South American didelphoids. In Clemens's (1966) excellent study of these with greatly augmented materials, he has raised two former subfamilies of Didelphidae to the rank of families, his *Pediomyidae* and *Stagodontidae*. If *Derorhynchus* and some other peculiar Paleocene South American genera and also, as Clemens agrees, *Caroloameghinia* and *Glasbius* (Clemens's genus from North America) are retained in Didelphidae, I think that *Pediomys* and *Didelphodon* (essentially the type of *Stagodontidae* despite the difference in names) likewise warrant no more than subfamily distinction. This is a minor point, but it has some importance in maintaining a reasonable balance of categorical levels.

⁴⁸ There are indeed distinct differences between the known Cretaceous marsupials and any Recent members of the order, as noted especially by Clemens (1966). However, reference by Clemens and others of some Cretaceous and Recent forms to the same subfamily, Didelphinae, recognizes extraordinary conservatism, much greater than is demonstrable for any other mammals.

not especially pertinent in this study, no placental carnivores appeared in South America until the late Pliocene. However, carnivorous marsupials were becoming differentiated from the didelphids in the Paleocene. In the Eocene they were already quite diverse and included definitely predaceous types. Some of the didelphids, strictly speaking, doubtless also included small live prey in their diets, as do a number of recent didelphines. In the middle and later Tertiary the borhyaenids had a large range in size and also in the extent and details of carnassial specialization. Between them and some didelphids, the ecological niches for carnivores seem to have been about as full as in North America or the Old World except Australia, and rather more so than in Australia. Most aberrant and remarkable were the thylacosmilines, convergent in great detail to the placental sabertooths, a habitus that never evolved in Australia as far as known.

NECROLESTIDAE. This family, unquestionably valid as such, is known by a single genus, probably a single species, and very few specimens. It is another vicar for insectivores, lacking as such in a phylogenetic sense in the South American faunas. It is closely convergent to the marsupial "mole," *Notoryctes*, of Australia and to the placental golden "moles," Chrysochloridae, of Africa. (Besides Patterson, 1958, see Scott, 1905.) Convergence to the true moles, Talpidae, of Eurasia and North America is not quite so close, but the ecological similarity is still great. Animals of similar adaptive facies survive on all other continents under climatic, edaphic, and community conditions present in South America, but there is nothing like it in South America now. This is another family, like the argyrolagids, that apparently should have survived. But it did not.

CAENOLESTIDAE. The Caenolestinae, only surviving group, are diminutive animals with procumbent, pinching incisors and broadly insectivore-like cheek teeth. They are in fact insectivorous and evidently

have shared that facies with some didelphids throughout the Cenozoic in South America.⁵¹ The Palaeothentinae and Abderitinae differ mainly in progressively greater development of shearing action in a cheek tooth immediately anterior to the triturating molars. This, with the Polydolopidae (below), represents rather close convergence in dentition (but not other anatomical features) to the "rat" kangaroos (bettongs, tungsos, squeakers, potoroos, etc., Potoroinae) of Australia, also to the phalangerid *Burramys*, most multituberculates, and some primates (see Simpson, 1933). The recent marsupials with such "plagiaulacoid" dentitions are all herbivores, and it has been inferred that the fossil animals of this facies but other taxa were also. They may, however, be some question as to where or whether in the caenolestoid series transition from insectivorous to herbivorous habits occurred. If it did occur, the specialized caenolestoids were ecologically more like some small rodents than like insectivores. All of them evolved before there were any Rodentia in South America. The polydolopids apparently became extinct before they had rodent competitors, but the Palaeothentinae and Abderitinae lived for a long time (at least Deseadan through Santacrucian) in communal associations with rodents.

POLYDOLOPIDAE. These animals represent the extreme of "plagiaulacoid" specialization in the caenolestoids, discussed above. Primitive conditions in a Paleocene polydolopid from Itaborai suggested to Paula Couto (1952) that the principal lower shearing tooth is not homologous in Polydolopidae and specialized Caenolestidae (mainly Abderitinae), although he continued to accept caenolestoid affinities for

⁵¹ Armadillos, also present from the Paleocene onward, are also largely insectivorous, and ant-eaters, from the mid-Tertiary, are exclusively so but with much more stringent restriction among insect prey. Thus although lacking Insectivora, South America has long had a full complement of insectivores.

the former. That has been generally accepted, by me among others, but on second thought I think that this evidence does not necessarily negate homology of the shearing teeth. In any case, whether independently evolved or not, the Polydolopidae do represent in more extreme form an adaptive trend, and hence probably an ecological habitus, exhibited in less specialized form in the Palaeothentinae and Abderitinae.

GROEBERIIDAE. The one, poorly known species is decidedly rodent-like in the lower jaw and dentition (Patterson, 1952). It is perhaps significant that placental rodents are not known in the same fauna, which may possibly antedate the arrival of rodents in that region (Simpson, Mino-prio, and Patterson, 1962). In any case, the origin of the Groeberiidae almost certainly occurred in the absence of Rodentia, and rodent competition could conceivably account for their extinction. However, they lived under ecological conditions evidently quite peculiar, although in an unknown way, and may have survived for some time, as they originated, without presently known record.

ARGYROLAGIDAE. This family needs no further characterization at this point. The purpose of the present conspectus is to show how wide was the adaptive radiation and ecological dispersal of marsupials in South America and that the argyrolagids add an evolutionary development that was markedly distinct, not only phylogenetically, but also adaptively and ecologically.

Faunal comparisons. In Tertiary South America, marsupials underwent a wide adaptive radiation that fitted them into some ecological roles played by placentals in all other continents with the incomplete exception of Australia. They occupied all the usual roles for carnivores, including the extreme sabertooth habitus (Thylacosmilinae) most of those for insectivores, including the extreme fossorial habitus (Necrolestidae), and some of those for rodents, including the extreme ricochetel habitus (Argyro-

lagidae). Also included were the extraordinarily adaptable didelphids, ranging from insectivorous to carnivorous, to frugivorous, or generally polyphagous. They have had a talent for survival and are, in fact, the only American marsupials that do survive except for a few, also rather generalized caenolestids.

That wide radiation took place in communities that also included even more numerous and more varied placentals. In ecologically balanced marsupial-placental faunas, roles were divided between those groups and the radiation of each was limited thereby. Marsupials did not evolve into fully herbivorous browsers and grazers, those niches being divided among the very numerous ungulates and some of the edentates. Marsupials never attained anything approaching the breadth and diversity of rodent adaptations, those being occupied early in part by small ungulates and later in enormous variety by rodents themselves. Arboreal insectivorous-frugivorous habits evidently occurred among some didelphids, and I suspect may have involved some more early specialized extinct marsupials not yet found or not recognized as belonging in these niches. These niches later were largely taken over by primates. Terrestrial insectivorous niches were divided among marsupials and edentates, as most of them still are.

In Australia, balanced mammalian faunas evolved with much less placental participation, and the parallel between marsupial radiations in Australia and South America is limited by that fact. Bats are abundant in Australia and are inferred to have been so for a long time, as also in South America. Although there are gliding phalangeroids in Australia,⁵² no known marsupials anywhere are really batlike. Rats (Muridae) have long been numerous and varied in Australia, and this seems to have inhibited the evolution, or survival, of ratlike mar-

⁵² It is curious that South America, with its great and varied forests, has no gliding mammals. It is the only continent without them.

supials since the Miocene, at least. There are, however, rodentlike, non-ratlike marsupials such as *Vombatus*. There are somewhat *Vombatus*-like true rodents in South America, but no marsupials of similar habitus. In over-all habitus the South American argyrolagids are more like the Australian placental *Notomys* than like any Australian marsupials, although there is some slight resemblance to small macropodids and, still more distantly, even to some peramelids. As noted above, insectivorous marsupials have been common in South America throughout the Cenozoic but have shared insect food with a number of placentals. In Australia most of the small dasyurids are at least partly insectivorous, and some are ecologically quite similar to small didelphids. One, the numbat (*Myrmecobius*), is a specialized anteater. (As with so-called anteaters in South America, numbats probably eat more termites than ants.) Even with the addition of the monotreme anteaters, these animals may never have been really abundant or diverse, and they do not balance the more common and highly varied ant and termite eaters in South America.⁵³ Bandicoots

⁵³ This rich food source is not exploited entirely by mammals in any region. Reptiles, birds, and often still other groups also share.

Numbats are now extinct over much of their range and are rapidly diminishing over the rest of it. This is largely, perhaps entirely, caused by human activities, not by direct onslaught but from modification of the environment, especially by bush fires (Wood Jones, 1923, pp. 126–127). This has a particular interest in that it shows that small, non-prey animals, exempted by Martin (e.g., 1958, 1966) from his general theory of human intervention as cause of Pleistocene-Recent extinction, can also be affected.

Wood Jones's classic account (*loc. cit.*) should be modified on two points: the statement that numbats are "probably phylogenetically senile" is meaningless in the light of present knowledge of adaptation and evolution; the quotation without dissent of a here anonymous opinion that *Myrmecobius* is actually an unmodified survivor of Jurassic marsupials is doubly wrong—there were no Jurassic marsupials, and *Myrmecobius* is not an unmodified, or even a moderately modified survivor of any Jurassic mammals.

(Peramelidae) are also partly insectivorous in a broad sense, although it is not evident that many of them depend entirely on insect food.

The major difference between South American and Australian marsupial radiations is that in South America all the medium-sized to large herbivores, including strict browsers and grazers, have been placentals throughout the Cenozoic whereas in Australia they have all been marsupials. In both faunas these animals have been among the most individually abundant and taxonomically varied, so that the faunas over-all have been and are very different in aspect in spite of the fact that both embrace wide-ranging marsupial radiations. The contrast is heightened by the fact that the Australian marsupial and the South American placental herbivores exhibit very little morphological convergence, although they have similar ecological roles.

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ADDENDUM

Since this study was sent to the editor several relevant publications and personal communications have been received. These importantly supplement the preceding text but do not require its substantial alteration. They are here discussed and references are given.

Distribution. Pascual *et al.* (1966, received in 1968) would modify the correlation and nomenclature of strata containing argyrolagids. They leave open the question whether the Chapadmalal Formation is later than the Monte Hermoso Formation or only of a different facies, but in any case maintain that the known mammalian faunas in those formations are not sufficiently distinct for recognition of different formal ages and stages. They therefore refer the Chapadmalal Formation to the Monte-Hermosan ("Montehermosense") stage, correlated with the early and middle Blancan of North America and considered late Pliocene as a whole. (Late Blancan is now generally considered Pleistocene; opinions differ as to whether any of the earlier Blancan should be referred to the Pliocene and if so, how much.)

Following a second thought by J. L. Kraglievich (1959), Pascual *et al.* (1966) now considered the Vorohué and San Andrés formations as inseparable and refer them (together) and a separate Barranca de los Lobos Formation to an Uquian ("Uquiense") stage, correlated with the

late Blancan as early Pleistocene. As noted earlier in the present study, *Microtragulus* occurs in those formations and may be added to their faunal list. It also occurs in the Huayquerian ("Huayqueriense"), a preferable name for the Araucarian, but not in Buenos Aires Province, to which the work of Pascual *et al.* (1966) is confined.

For the most part, collectors used the formational terminology of J. L. Kraglievich (1952), which, whether accepted as definitive or not, does place the specimens in real and published rock sequences. It therefore still seems best to retain those distributional data, as I have in this publication. The exact placing of the Pliocene-Pleistocene boundary remains moot in South America and indeed everywhere else. The different placing of it by Pascual *et al.* (1966) does not significantly alter the indicated known span of the Argyrolagidae, from probable middle Pliocene to at least early and possibly middle Pleistocene.

Classification. Ringelet (1966, received in 1968), in the same volume as Pascual *et al.* (1966), has redefined family and genus and figured a previously unpublished specimen. She considers Argyrolagidae Ameghino, 1904, a synonym of Microtragulidae Reig, 1958; *Argyrolagus* Ameghino, 1904, a synonym of *Microtragulus* Ameghino, 1904; and *M. argentinus* Ameghino, 1904, a synonym of *A. palmeri* Ameghino, 1904. Reasons for not accepting those synonymies have been adequately discussed here on previous pages. Ringelet's family definition is valid for the taxon I call Argyrolagidae, except for the subsequent discovery that metatarsals III and IV are not in fact fused. Her generic definition, as regards mandible and dentition, is essentially a summary description of the previously undescribed specimen, figured by her in plate X, figs. I and J. It is in that respect a useful supplement but of course does not apply to the specimens, species, and genera of the whole family. The description, original in Spanish, may be translated as follows:

“Mandibular ramus short and high, flat internally, lightly convex externally, with lower border very convex; anterior border of the masseteric crest strongly marked. Dental formula $\overline{2.0.1.4}$. I_1 large, compressed, hypsodont, reniform in section, convex externally and concave internally, implanted anteroposteriorly in the same line as the molariform series, so that the incisive border is very narrow, intra-alveolar part near the lower border parallel to the mid-line of the symphysis. I_2 approximately ovoid in section, with the internal face somewhat flatter, size similar to I_1 . P_3 (?) separated from I_2 by a diastema approximately a little less than the diameter of the two incisors, small, triangular in section, approximately isosceles with the base posterior, with rounded angles, implanted obliquely postero-externally. Molars octodontiform, with peripheral cusps of doubtful homologies, the coat of enamel becoming thin and almost disappearing on the anterior fold and on the inner side of the posterior face. M_{1-3} subequal, with the anterior lobe (trigonid) larger than the posterior (talonid), triangular in section, with approximately equal sides; posterior lobe compressed anteroposteriorly. M_4 smaller, with the posterior lobe narrower than the anterior but less compressed anteroposteriorly than on the other molars. M_{1-2} somewhat imbricated, with the anterior somewhat displaced externally.”

Dr. Rosendo Pascual (personal communication, 25 February 1969) has kindly added the information that this specimen is in the Museo de la Plata and was collected in 1961 in the Chapadmalal-Miramar region in the cliffs of the Playa de las Palomas, a little north of the Balneario Chapadmalal, in beds designated by J. L. Kraglievich (1952) as belonging to the Chapadmalal Formation. Pascual adds the following measurements and descriptive notes (here translated):

“Height of mandibular ramus on the external face below the first cheek tooth. . . . 4.3 mm.

TABLE 3. RELATIVE LENGTHS OF SOME PELVIC DIMENSIONS IN CERTAIN MARSUPIALS AND RODENTS.

- A. Postacetabular (to the ischial spine) length as a percentage of preacetabular (iliac) length.
 - B. Length from center of acetabulum to center of sacral attachment as a percentage of length from center of sacral attachment to anterior end of ilium.
- Figures are from single specimens and may vary considerably in the species and genera.

Species	A	B
<i>Argyrolagus scagliai</i>	54	88
<i>Caenolestes obscurus</i>	51	206
<i>Dipodomys merriami</i>	62	117
<i>Allactaga mongolica</i>	81	109

SUPPLEMENT TO TABLE 3
(Ratio B not taken)

	A
<i>Antechinomys spenceri</i> , single male skeleton	59
<i>Notomys mitchelli</i> , four skeletons.	Range 52–56 Mean 53.5

“Height of manibular ramus on the external face below the third cheek tooth. . . . 5.3 mm.

“Length of distance from anterior face of the first incisor to the last cheek tooth along the alveolar border. . . . 11.8 mm.

“Length of space occupied by the cheek teeth along the alveolar border. . . . 7.8 mm.

“The anterior incisor extends within the alveolus to beneath the third cheek tooth (its open base is visible). The symphyseal surface extends to beneath the anterior face of the second cheek tooth (the first of those bilobate). Posterior to the last cheek tooth two small foramina can be discerned, one behind the other, which might possibly belong to a very small shed molar. However, the posterior expansion of the talonid of the last cheek tooth preserved makes me think that there was no additional molar. The masseteric crest projects very strongly and stops abruptly at mid-height

of the mandibular ramus, below the posterior lobe of the penultimate molar present."

This specimen belongs to the genus to which the name *Argyrolagus* is somewhat arbitrarily applied in the present study. Specific reference is doubtful on the data available, but should be possible with further study of the original. Dr. Pascual has kindly arranged for such study, but it has been decided not to delay the present publication for that purpose.

Affinities. Dr. John Kirsch (1968) has now published a summary of his new classification of marsupials, based largely but not exclusively on serological evidence. In still more succinct form, his arrangement is as follows:

Superorder Marsupialia

Order Polyprotodonta

Suborder Didelphimorphia

Superfamily Didelphoidea

Superfamily Borhyaenoidea

Suborder Dasyuromorphia

Superfamily Dasyuroidea

Suborder Pamelemorphia

Superfamily Perameloidea

Order Paucituberculata

Superfamily Caenolestoidea

Order Diprotodonta

Superfamily Vombatoidea

Superfamily Phalangeroidea

Superfamily Tarsipedeoidea

This represents a truly important contribution, especially as regards affinities within his Diprotodonta (details not given here), but it would only impede any placing of the Argyrolagidae, not listed by Kirsch. I do not see how they could reasonably be put in any of his orders, still less reasonably in any lower taxon. The alternative within that framework would be to erect still another order for the argyrolags alone. That seems to me unjustified on balance and at present, and I hope that it does not tempt any nomenclator. I still

feel that for overall use, including extinct groups, it is impractical or undesirable to try to establish taxa of categorical rank between superfamilies and Marsupialia even though a reasonable case on the basis of living forms has been made (by Ride as well as Kirsch) for subdivision into several orders.

Kirsch's inclusion of Perameloidea in Polyprotodonta is also, but less essentially, relevant to the present study. It is based on his finding closer serological resemblances between Perameloidea and Dasyuroidea than between either and Phalangeroidea. If that is a reliable *phylogenetic* indicator, then we must conclude that typical and complete syndactyly, contrary to my conclusion in the body of this paper, has in fact arisen quite independently twice among the Marsupialia. In support of this possibility, Kirsch has also pointed out (in personal communication) that incipient syndactyly was long ago reported in the Didelphidae.⁵⁴ He kindly sent me a photograph of the hind foot of *Caluromys derbianus* to illustrate this tendency. The photograph shows digits II and III nearly (not quite) equal and less divergent than the other digits, but apparently without

⁵⁴ Bensley (1903) said of *Marmosa* that "there is here, in some species, an indication of the syndactylous condition of the Phalangeridae," and that the conditions in *Marmosa* "are repeated in *Caluromys*." His figure of the pes of *Marmosa priscilla* (pl. 7, fig. 7) is almost exactly like that of *Dromicia nana* (pl. 7, fig. 13), and the latter was in fact probably another specimen of *M. priscilla*. In both, digits II and III are subequal and appressed, but they do not appear syndactylous and they are very unlike any phalangerid. In his diagnosis of *Marmosa*, Tate (1933) included, "Almost no trace of syndactyly." That implies that there is *some* trace. Being given as diagnostic, it might also imply that a more definite trace occurs in some allied genus, but I do not find a statement to that effect in Tate's work. Another paper (Tate, 1939) in which he explicitly discussed both *Marmosa* and *Caluromys* says nothing about syndactyly in either one. It is perhaps not surprising that little attention has hitherto been paid to these hints of incipient syndactyly in didelphids.

TABLE 4. LENGTHS (IN MILLIMETERS) AND PROPORTIONS OF LIMB BONES IN AN ARGYROLAGID, SOME MARSUPIALS, AND SOME RODENTS (EXCEPT AS INDICATED BELOW, ALL MEASUREMENTS ON SINGLE ADULT SPECIMENS).

Taxa	A Humerus	B Radius	C Femur	D Tibia	E Metatarsus	A/B	C/D	D/E	A/C	(A+B)/ (C+D)
Argyrolagidae:										
<i>Argyrolagus scagliai</i>	ca. 17½	ca. 18½	43.9	60.4	35.6	ca. .94	.73	1.69	ca. .40	ca. .35
Caenolestidae:										
<i>Caenolestes obscurus</i>	13.9	15.0	14.3	22.3	8.6	.93	.64	2.59	.97	.79
<i>Rhyncholestes raphanurus</i>	14.0	15.5	15.3	22.6	8.6	.90	.68	2.63	.91	.79
Dasyuridae:										
<i>Antechinomys spenceri</i> *	13.8	20.9	20.8	29.0	15.3	.66	.72	1.90	.66	.78
Macropidae:										
<i>Bettongia lesueuri</i>	34	42	81	114	40	.81	.71	2.85	.42	.39
<i>Petrogale penicillata</i>	70	87	147	187	58	.80	.79	3.22	.48	.47
Heteromyidae:										
<i>Dipodomys merriami</i>	11.7	14.9	23.9	34.3	17.0	.78	.70	2.03	.49	.46
Dipodidae:										
<i>Allactaga mongolica</i>	14.3	17.7	34.1	49.8	32.5	.81	.68	1.53	.42	.38
<i>Jaculus</i> sp.	15.7	—	39.5	58.3	40.0	—	.68	1.46	.40	—

* Data for this species are means for seven preserved (not skeletonized) specimens measured on X-ray films. Even as means, these cannot be as accurate as direct measurements on bones, but they are believed to suffice for present comparative purposes. The specimens belong to the Western Australian Museum. The radiographs were taken by Basil Marlow at the Australian Museum at the instance of W.D.L. Ride especially for the present study.

SUPPLEMENT TO TABLE 4

	A	B	C	D	E	A/B	C/D	D/E	A/C	(A+B)/ (C+D)
<i>Antechinomys spenceri</i> , single male skeleton	16.8	24.8	22.8	34.6	6.19	.64	.66	1.82	.74	.72
<i>Notomys mitchelli</i> , single female skeleton	14.7	17.3	25.5	35.7	17.9	.85	.71	2.00	.58	.50

common integument beyond the metatarsals. This is not clear or developed syndactyly, even though it could well represent a primitive basis for evolution of syndactyly. There is also the fact, well known but overlooked by me when I wrote earlier parts of this study, that the placental *Potamogale* has advanced syndactyly (see

e.g., Walker *et al.*, 1968, figure on p. 118) closely similar to that of the Phalangeroidea and certainly of completely independent origin. Since that condition has arisen in two groups by pure convergence, it could have arisen two or more times by parallelism within the Marsupialia. The question of possible independent

origin of syndactyly in Perameloidea and Phalangeroidea must thus still be considered open, but this does not particularly weaken my previous conclusions that the Argyrolagidae were not derived from or specially related to either group. First, all known members of both those groups are indeed syndactylous, and it seems quite certain that no ancestor of the Argyrolagidae ever was, even to an incipient degree. Second, evidence against such relationships is supported by this point, but includes so much else as to be reasonably conclusive even without it.

Biology. Since this paper was written, a visit to the National Museum of Victoria, Melbourne, Australia, permitted me to make measurements on a skeleton of *Antechinomys spenceri*, more reliable than the x-ray data in Table 4, and to add homologous data for *Notomys mitchelli*. At La Trobe University, near Melbourne, live specimens of both species were observed through the kindness of Miss Meredith Stanley. *N. mitchelli*, like most *Dipodomys*, has a slow quadrupedal walk, a fast bipedal walk, a bipedal ricochet, and a startle reaction straight up.

In the following supplements, measurements are as in the previous tables under the same alphabetical designations.

It is confirmed that *Antechinomys* has a relatively longer forelimb than in the definitely bipedal forms and that its radius is peculiarly long relative to its humerus. The limb proportions of *Notomys* are close

to those of *Dipodomys*, and these two only distantly related rodents are remarkably similar in appearance, habits, and anatomy throughout. Either one probably gives a fair idea of what *Argyrolagus* was like when alive, even though they are placentals and it was a marsupial.

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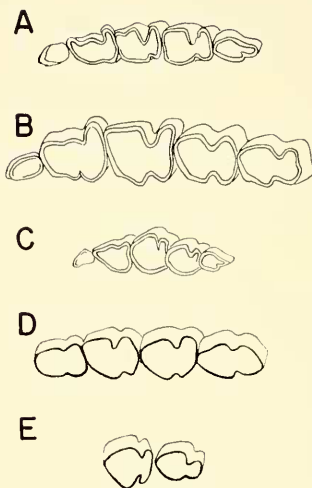


Figure 1. Crown views of right lower cheek teeth of Argyrolagidae. A, *Microtragulus reigi*, MMMP No. 960-M, P_3 - M_4 . B, *Argyrolagus scagliai*, MMMP No. 741-M, P_3 - M_4 . C, *Microtragulus catamarcensis*, MACN No. 5529, P_3 - M_1 . D, *Argyrolagus palmeri*, type, M_{1-4} , after Kraglievich (1931), reversed from left side. E, ?*Argyrolagus parodii*, type, M_{3-4} , M_3 after Rusconi (1936) and M_4 after Rusconi (1933), both reversed from left side. All $\times 4$.

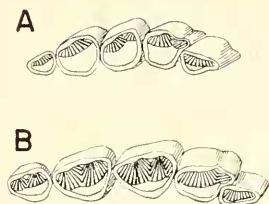


Figure 2. Crown views of right P_3 - M_4 of Argyrolagidae. A, *Microtragulus reigi*, MMMP No. 661-S. B, *Argyrolagus scagliai*, MMMP No. 785-S. Both $\times 4$.

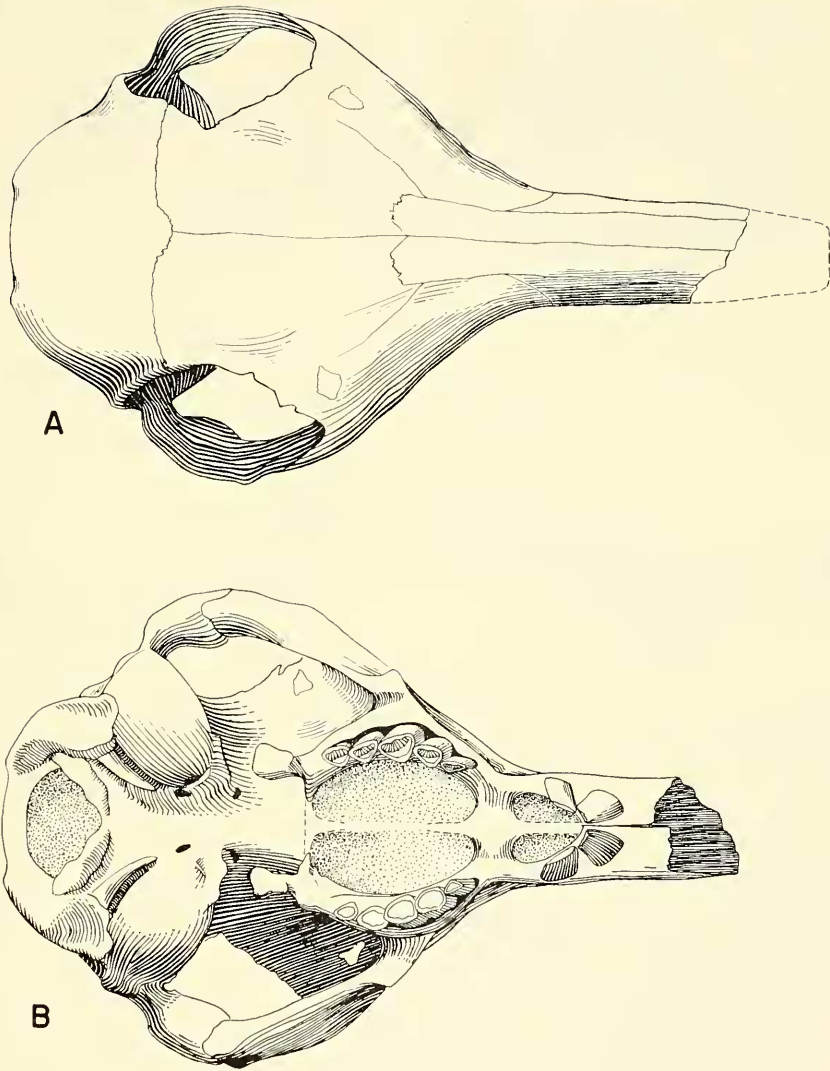


Figure 3. *Argyralagus scagliai*, MMMP No. 785-S, skull. A, Dorsal view. B, Ventral view. In this and the following figures of the skeleton of this individual, some restoration has been made by reversing to one side parts present on the other side and some distortion has been modified. Both $\times 2$.

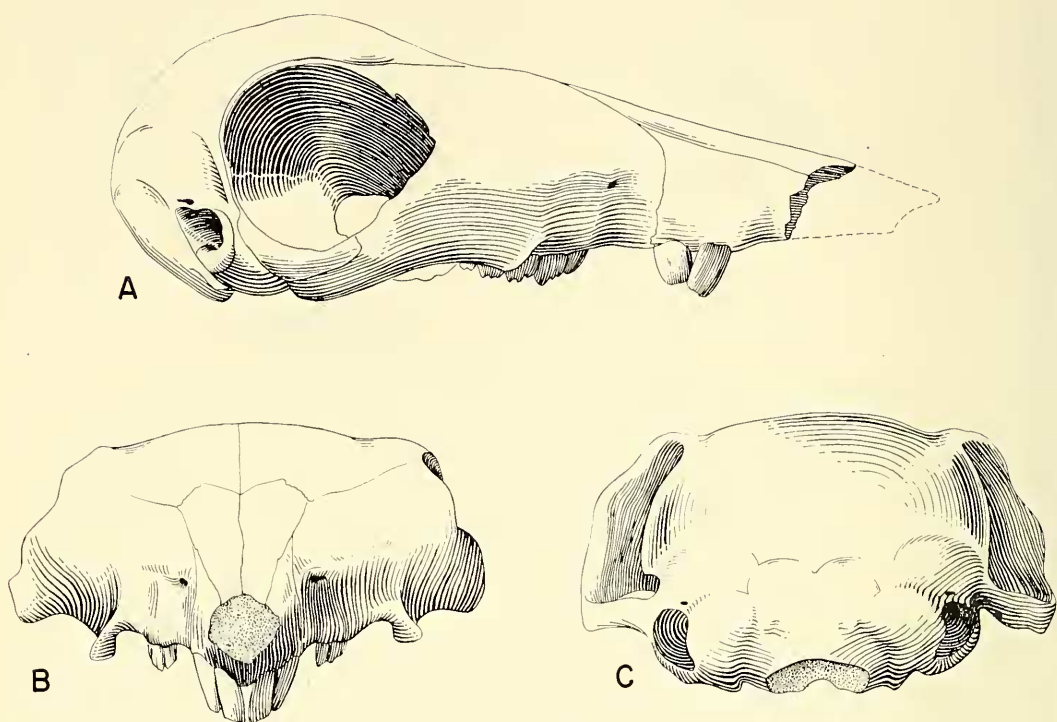


Figure 4. *Argyralagus scagliai*, MMMP No. 785-S, skull. A, Right lateral view. B, Anterior view. C, Posterior view. Snout in broken outline in A is hypothetical but suggested by known part in *Microtragulus reigi*. In B the broken snout has not been restored. All $\times 2$.

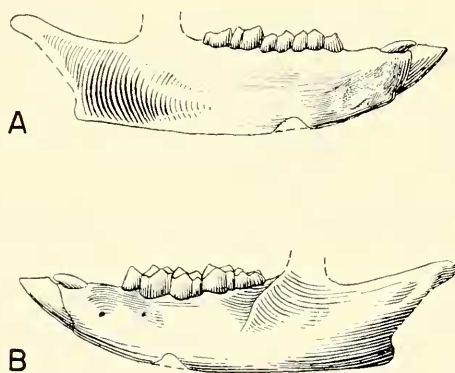


Figure 5. *Argyralagus scagliai*, MMMP No. 785-S, left ramus of mandible. A, Medial or lingual view. B, Lateral or labial view. The posterior part of this specimen is distorted by breakage and has been reconstructed with reference to occlusion with upper teeth of the same individual and placing of the condyle of the lower jaw on the glenoid surface of the skull. Both $\times 2$.

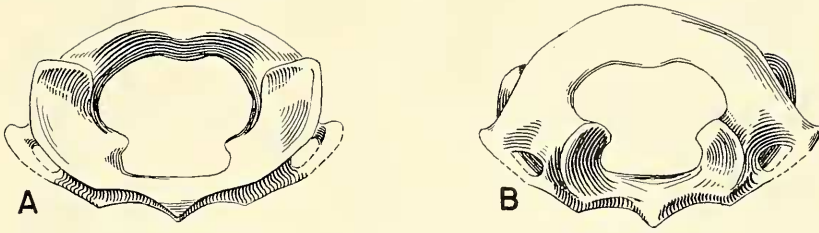


Figure 6. *Argyrolagus scagliai*, MMMP No. 785-S, atlas. A, Anterior view. B, Posterior view. Both $\times 4$.

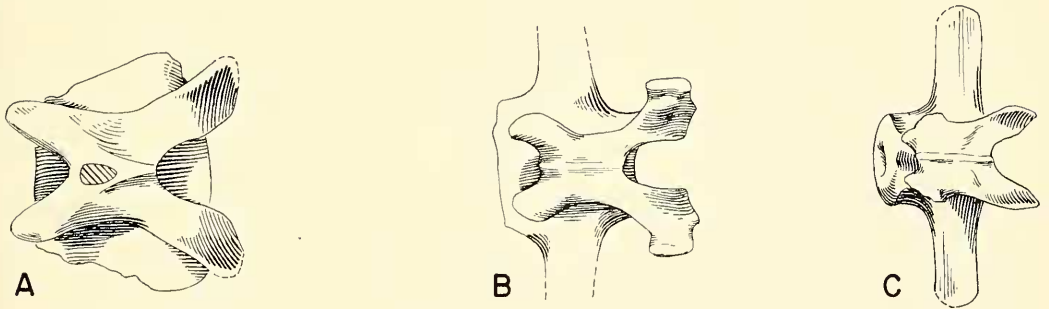


Figure 7. Dorsal view of anterior caudal vertebrae of Argyrolagidae. A, B, *Argyrolagus scagliai*, MMMP No. 785-S. C, Vertebra preserved with and possibly belonging to MACN No. 7130, type of *Microtragulus argentinus*. All $\times 4$.

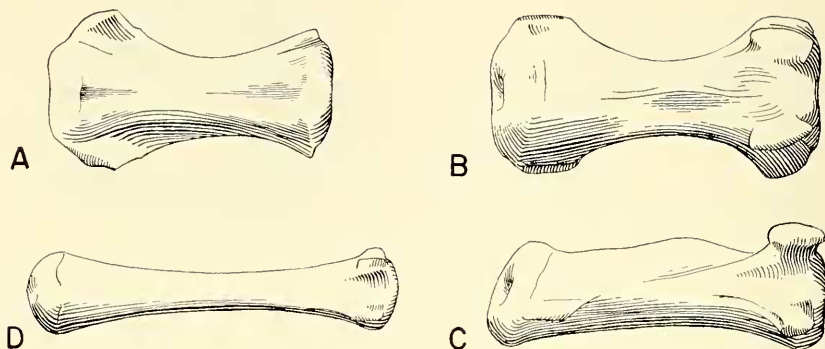


Figure 8. *Argyrolagus scagliai*, MMMP No. 785-S, medial to posterior caudals. A, Relatively anterior, probably first after kind of vertebrae shown in Fig. 7A, B, ventral view. B, More posterior vertebra, dorsal view. C, Same as B, right lateral view. D, Still more posterior vertebra, right lateral view. All $\times 4$.

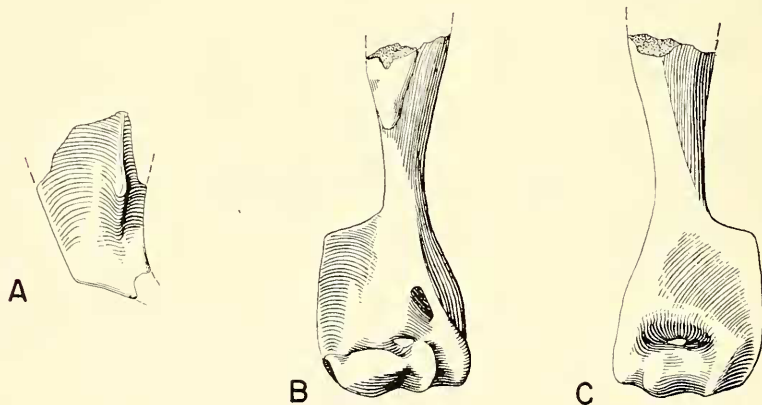


Figure 9. *Argyrolagus scagliai*, MMMP No. 785-S. A, Fragment of lower end of right scapula, lateral view. B, Right humerus lacking proximal end, anterior view. C, Same as B, posterior view. All $\times 3$.

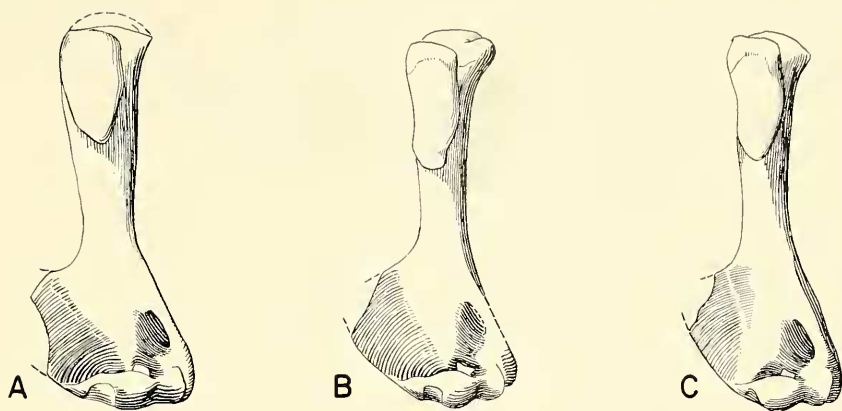


Figure 10. Anterior views of right humeri of Argyrolagidae. A, MMMP No. 795-S. B, MMMP No. 396-M. C, MMMP No. 395-M. For possible identifications see text. All $\times 3$.

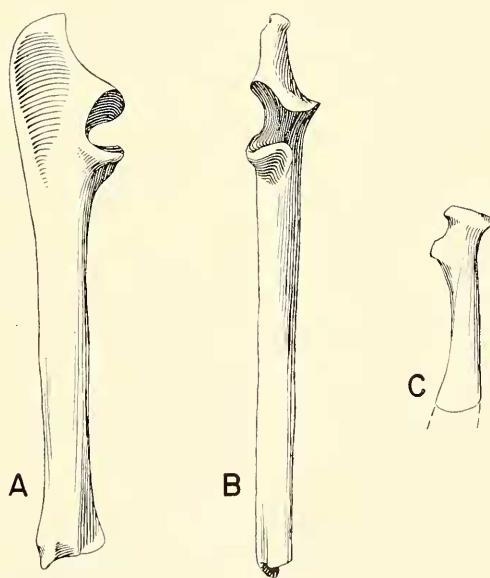


Figure 11. *Argyrolagus scaglioi*, MMMP No. 785-S. A, Right ulna, lateral view. B, Same as A, anterior view. C, Proximal end of right radius, anterior view. All $\times 3$.

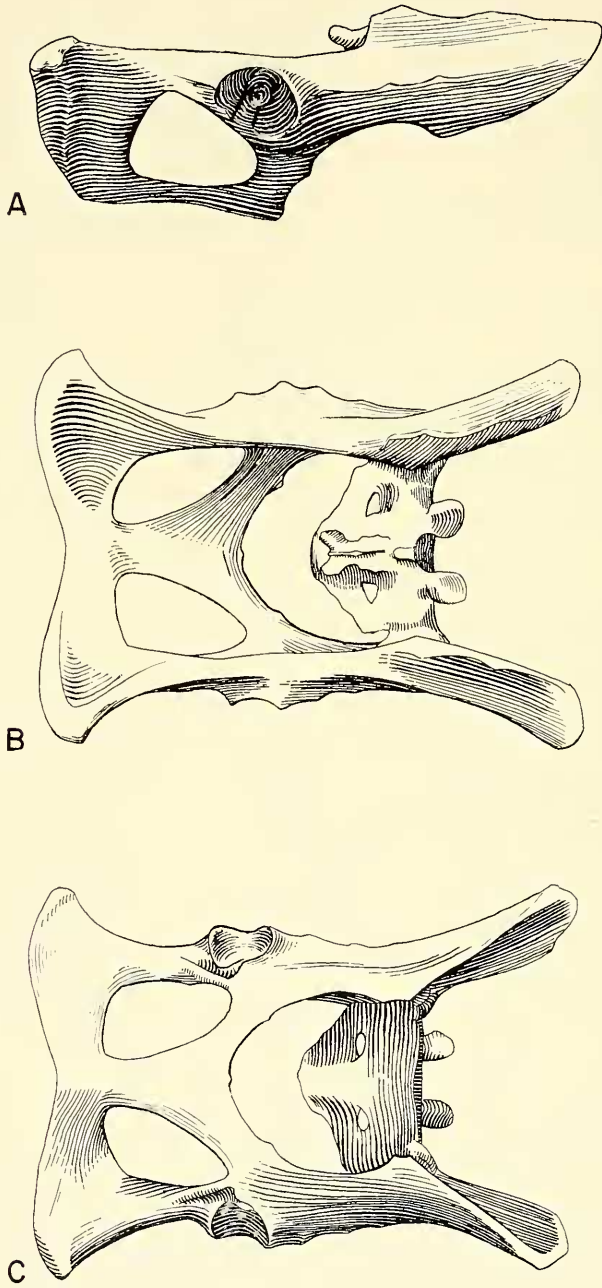


Figure 12. *Argyrolagus scagliai*, MMMP No. 785-S, sacrum and pelvis. A, Right lateral view. B, Dorsal view. C, Ventral view. All $\times 2$.

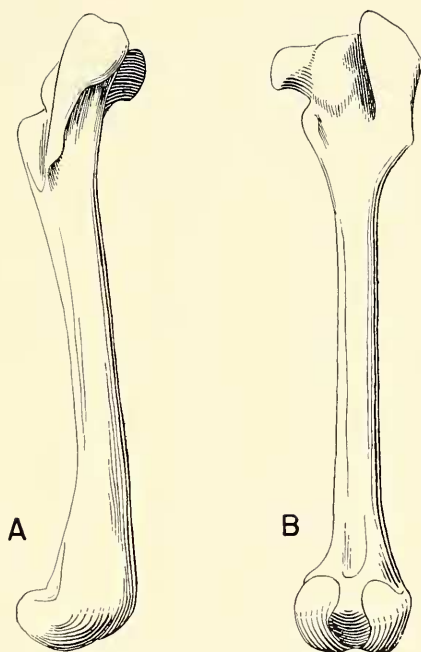


Figure 13. *Argyrolagus scagliai*, MMMP No. 785-S, right femur. A, Lateral view. B, Posterior view. Both $\times 2$.

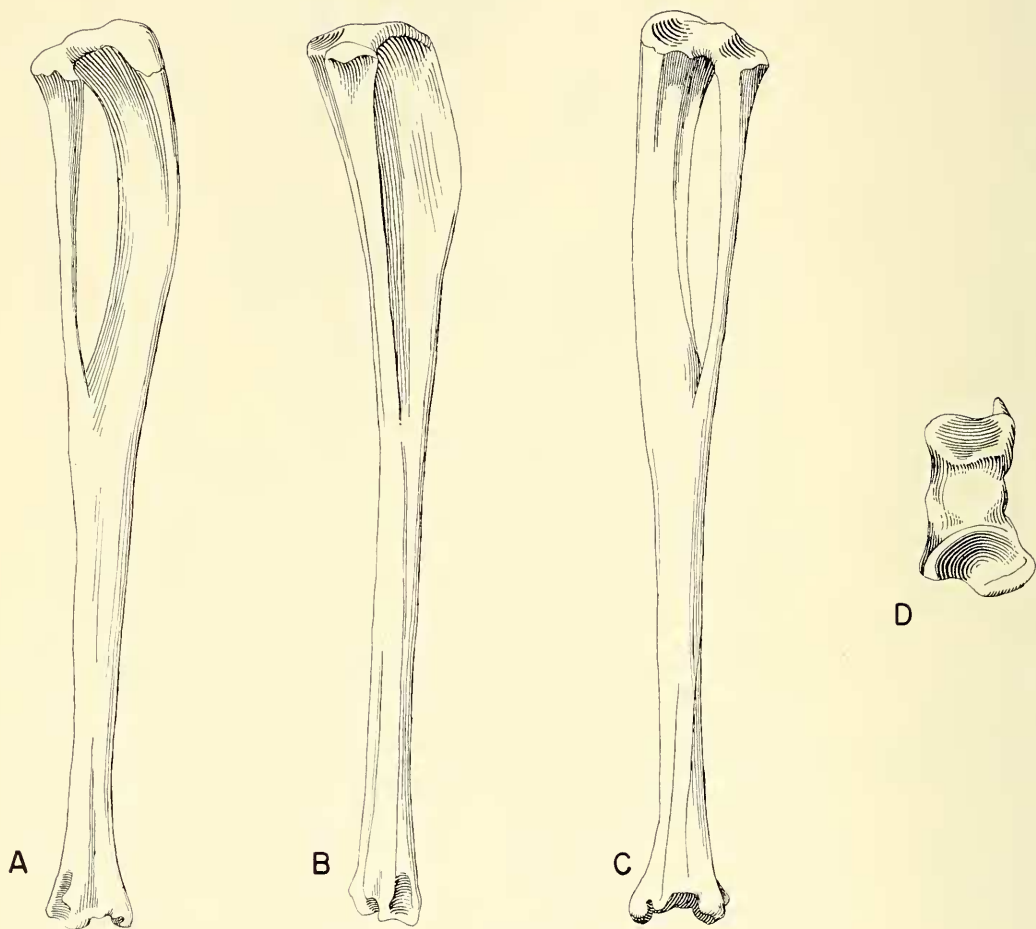


Figure 14. *Argyrolagus scaglioi*, MMMP No. 785-S, right tibio-fibula. A, Anterior view. B, Lateral view. C, Posterior view. D, Distal view. A, B, C $\times 2$. D $\times 4$.

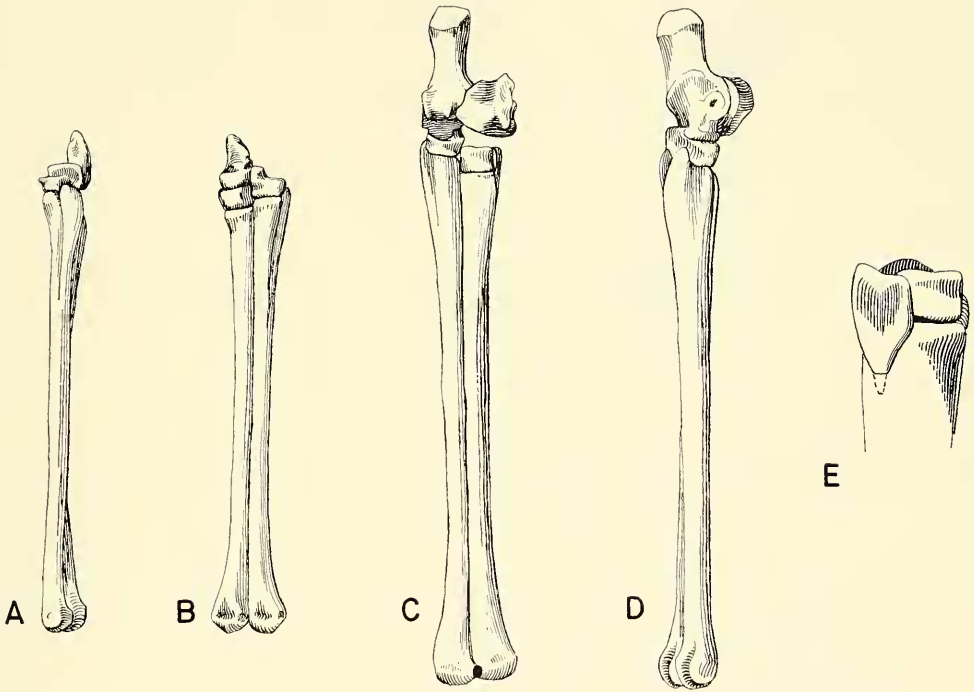


Figure 15. Tarsals and metatarsals of Argyrolagidae. A, *Micratragulus argentinus*, MACN No. 7130, left scaphoid, ectocuneiform, cuboid, and metatarsals III-IV, lateral view. B, Same as A, anterior (or dorsal) view. C, *Argyrolagus scagliai*, MMMP No. 785-S, right calcaneum, astragalus, cuboid, ectocuneiform, and metatarsals III-IV, anterior (or dorsal) view. D, Same as C, lateral view. E, Same individual as C-D, medial view of vestige of metatarsal II, ectocuneiform, and proximal end of metatarsal III. A-D $\times 2$. E $\times 4$.

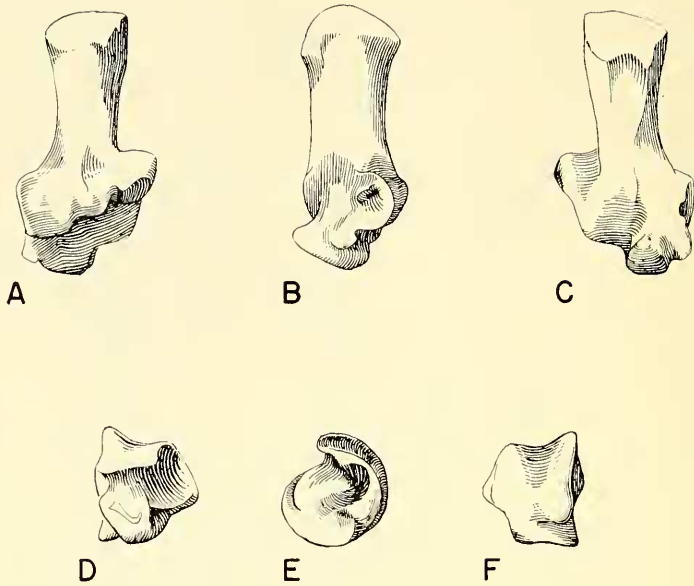


Figure 16. *Argyralagus scagliai*, MMMP No. 785-S. A, Right calcaneum, dorsal view. B, Same as A, lateral view. C, Same as A, ventral view. D, Right astragalus, ventral view. E, Same as D, lateral view. F, Same as D, dorsal view. All $\times 4$.

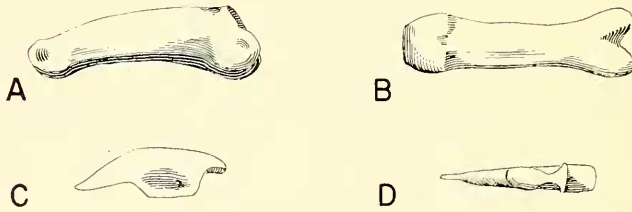


Figure 17. *Argyralagus scagliai*, MMMP No. 785-S. A, Proximal phalanx, medial view. B, Same as A, ventral view. C, Distal phalanx, medial view. D, Same as C, ventral view. All $\times 4$.

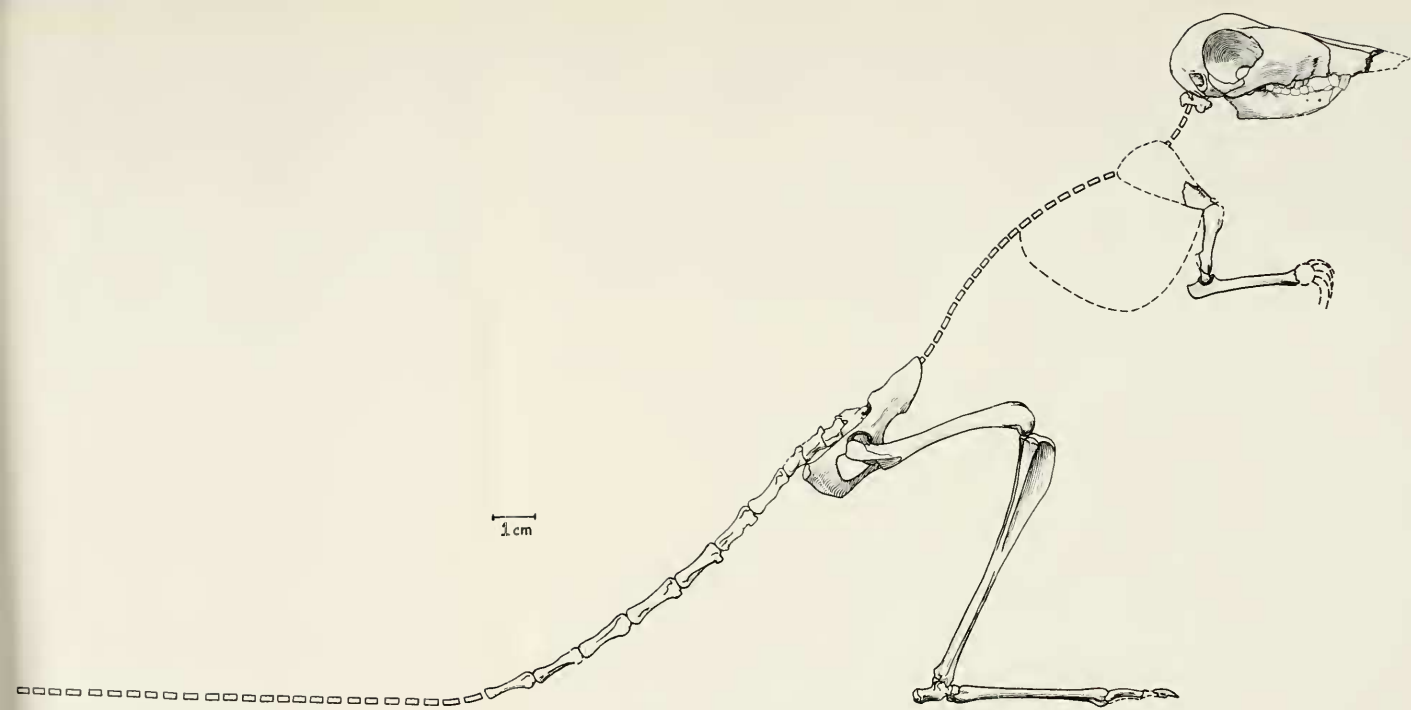


Figure 18. *Arguuiagrus sagittalis*, MMMP No. 785.5, skeleton, right lateral view. Parts shown shaded are in solid outline are preserved, although some there has been restoration from the other side. The rectangles in the line of the vertebral column are a conventional means of tying the skeleton together and are not intended to represent the missing vertebrae in size, shape, or number. The animal is shown in stationary plantigrade posture, inferred from analogy with *Dipodops*. From this pose the animal could leap vertically if startled or could move off by digitigrade re-archeing.

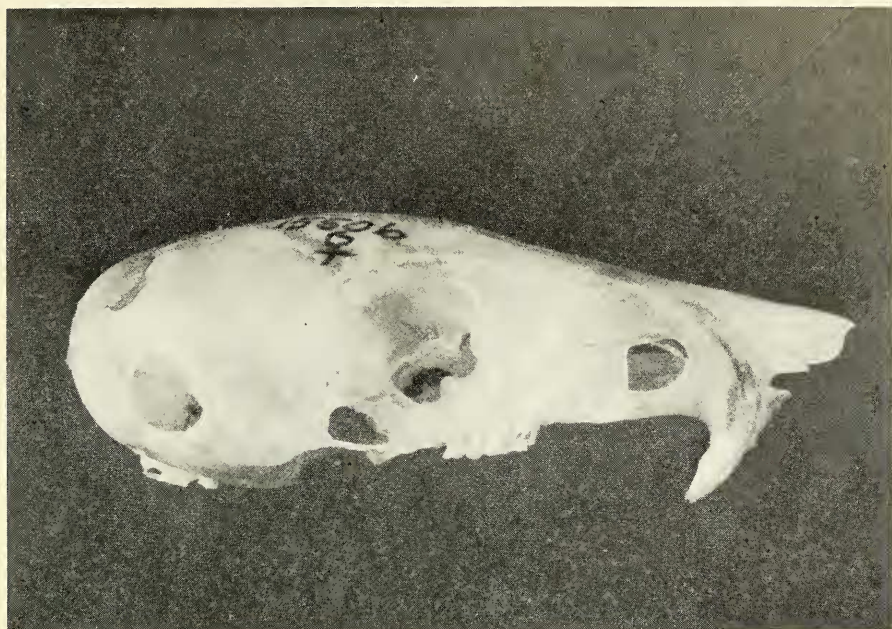


Plate 1. Above. *Dipodomys merriami*. University of Arizona, Zoology No. 15506. Skull. Right lateral view. Ca. $\times 2$. Below. *Microtragulus reigi*. MMMP No. 691-S. Skull. Right lateral view. Slightly less than $\times 2\frac{1}{2}$. This and the following two plates illustrate the extraordinary adaptive similarity in these two groups, which evolved from entirely different ancestors.

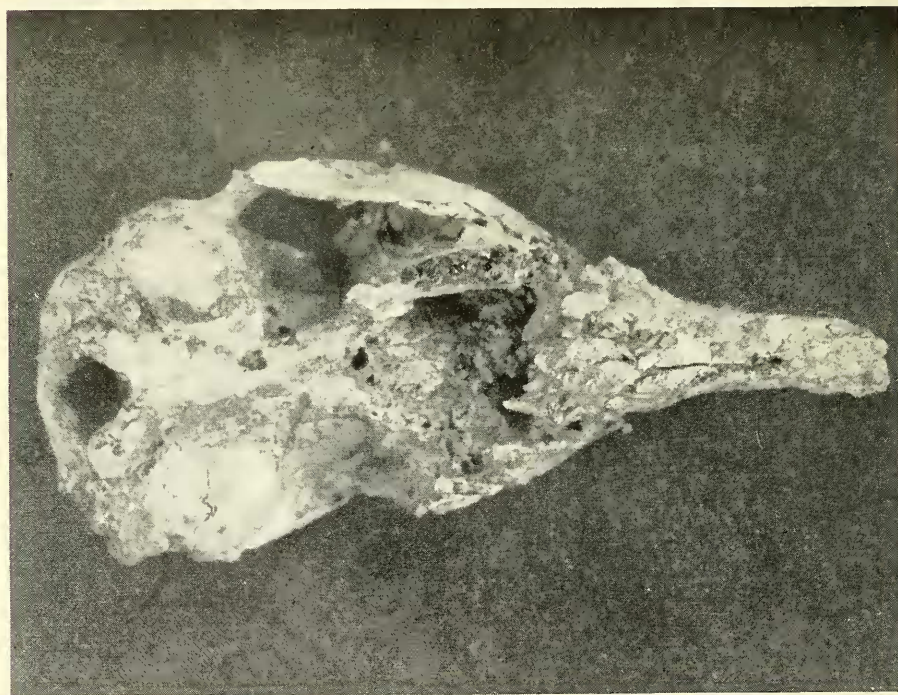
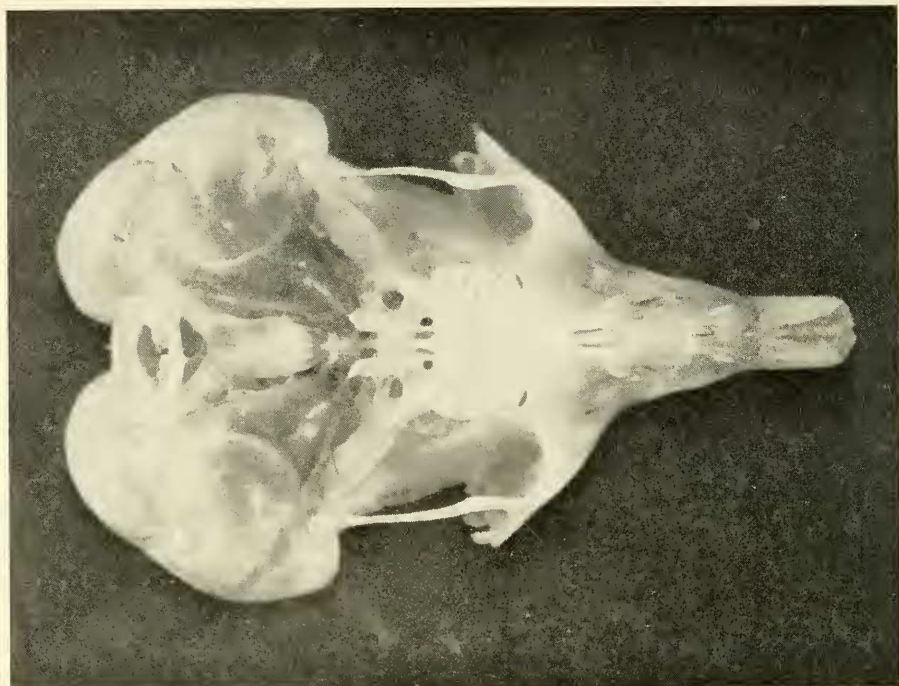


Plate 2. Same specimens and enlargements as Plate 1. Ventral views.

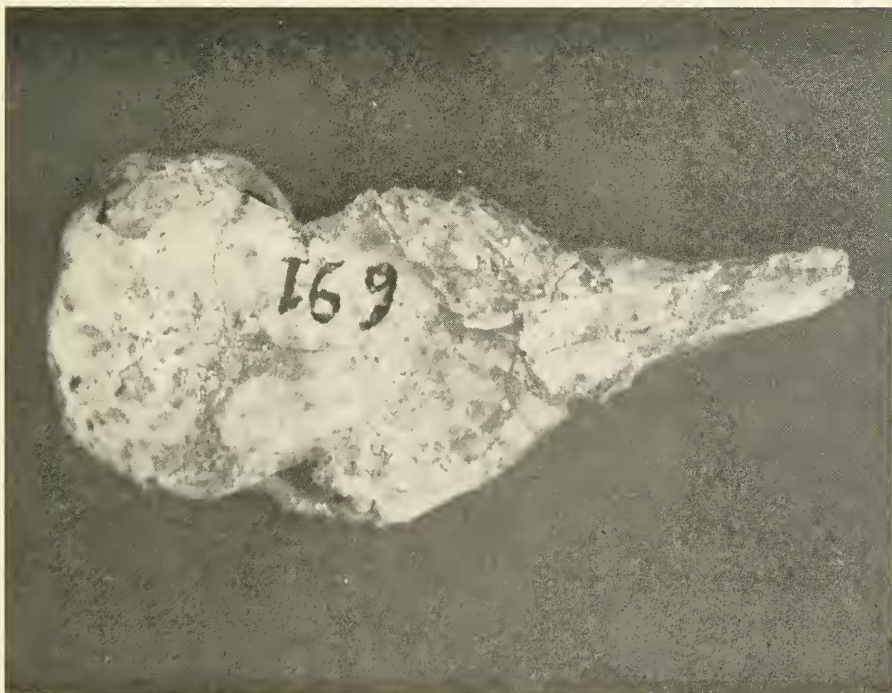
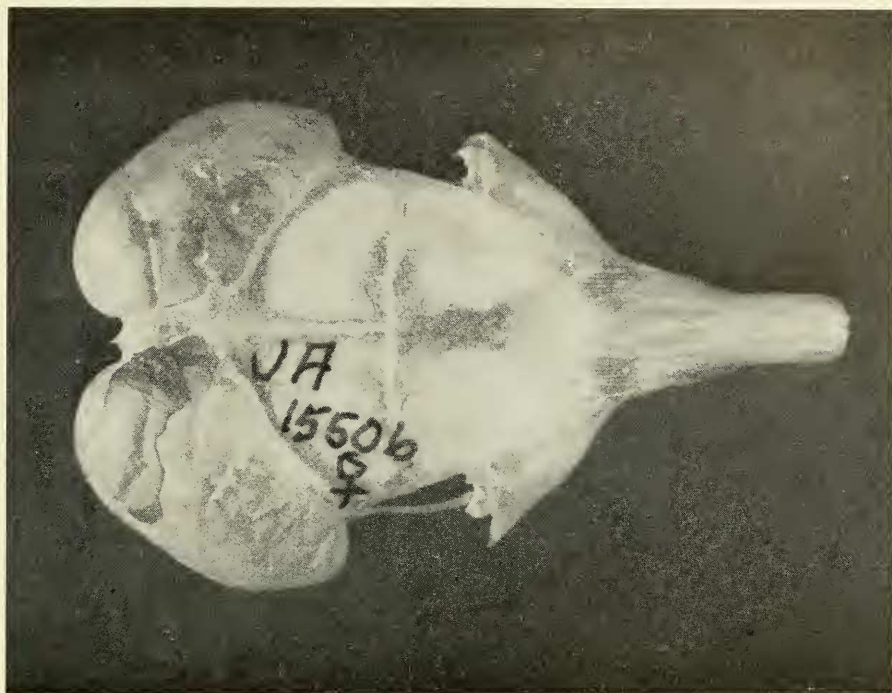


Plate 3. Same specimens and enlargements as Plate 1. Dorsal views.

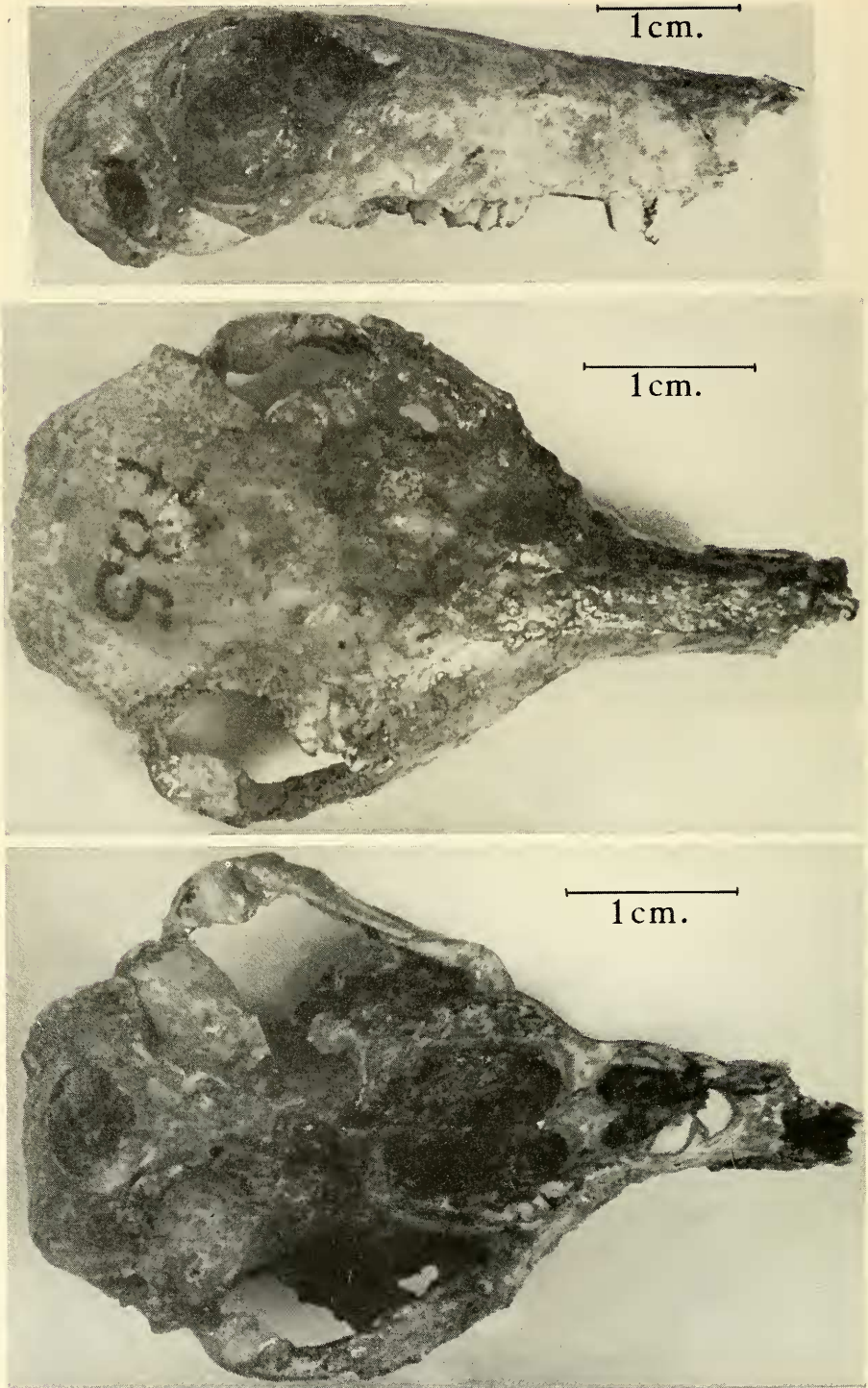


Plate 4. *Argyrolagus scagliai*. MMMP No. 785-S. Skull. Right lateral, dorsal, and palatal views. Photographs supplied by Dr. O. Reig.